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### THE AMERICAN SPECIES OF *SARCOSTEMMA* R. BR. (ASCLEPIADACEAE)\*

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As subjects for monographic study the Asclepiadaceae have been rather generally neglected since the beginnings of taxonomy. This may have been due, in part perhaps, to their minor economic importance and to the impression that genera in the family are easy neither to define nor to determine. A more important factor, however, has been the prevalent opinion that the flowers are so complex morphologically as to render the plants very difficult to study. One cannot deny with candor that these points are well-taken, but the result has been that no satisfactory general account of the family exists, making identification extremely arduous. Many ill-correlated small genera have been described because of their presumed uniqueness; and the vast potential of absorbing morphologic and ecologic topics in this interesting group has not been appreciated.

I was led to consider the Asclepiadaceae because of my interest in their adaptations for insect pollination and the bearing which this has on their phylogeny. It is remarkable that the pattern of evolution and the taxonomic difficulties encountered in this family and in the Orchidaceae are very similar. Except for certain differences which will be discussed below, these two families, the most specialized for insect pollination in Dicotyledones and Monocotyledones respectively, show similar developments in floral structure, aggregation of the pollen into pollinia, and a bewildering array of forms which almost defy classification. In many respects, however, the Asclepiadaceae are much the more specialized with regard to structure of the pollinium and the method of pollination. And their floral evolution, though to a certain extent parallel with that of the orchids, has been along slightly different lines. For example, the Asclepiadaceae are constructed upon a basic pattern of actinomorphy, in contrast to the strongly zygomorphic orchids. To what

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extent can we attribute these similarities and differences to the intimate relationship between the plants and their insect pollinators?

It soon became apparent that a study of these subjects can only be based on a dependable taxonomic system and a clear understanding of the morphology of the structures involved. With these points in mind, an investigation of *Sarcostemma* was undertaken as an introduction to the complexities of tropical American Asclepiadaceae. Not without a thorough review of all the genera, however, can the ideals of a sound morphology and taxonomy be realized, and it is not suggested that this account of one genus is more than an introduction to a program that would require years of study to complete.

*Sarcostemma* probably has been the least neglected of the genera in its alliance, for the plants are attractive both scientifically and esthetically. In the New World, the species are vines with umbelliform or racemiform inflorescences of fragrant, showy flowers. The flower, with the waxy corona bladders in the center, somewhat resembles that of the wax plant, *Hoya*, in those species with rotate corollas. The species of the group formerly assigned to *Philibertia*, which have campanulate flowers, were often cultivated in English greenhouses of the past century. And still fairly common in collections of succulents are the leafless African and Asian species, which occasionally produce clusters of yellow or green flowers.

In this paper, the New World species of *Sarcostemma* have been studied monographically; and, in order to maintain perspective, the Old World forms are treated synoptically. Unfortunately, the paucity of specimens and the general nomenclatural confusion of the Eastern Hemisphere species make it impossible to gain any understanding of their relationships, or even to estimate the number of species involved. It is possible that the evolutionary development of these species of the drier parts of the tropical and subtropical regions of the Old World has been along different lines from that of the New World forms. At any rate, many rather obscure genera are confused in the literature, and also, the misapplication of such names as *viminale* and *aphyllum* for leafless plants, throughout most of the Old World floristic accounts, has created a situation of extreme taxonomic chaos. A number of leafless species of *Euphorbia* have been confused with the sarcostemmas so that it is by no means easy to decide which family is being discussed in a given treatment.

With the detailed knowledge of the American species in mind, I have begun a reinvestigation of the morphology of the flower in the tribe Asclepiadeae. The results of such a study can be used as a basis for a classification of genera and species enabling one to view them as a whole and helping to remove that impression of chaos which has discouraged so many.

#### HISTORY OF THE GENUS

I do not propose to record in detail the history of the various species which have been attributed to *Sarcostemma* and its segregates. It seems desirable, however, to chronicle briefly those genera which have been related nomenclaturally. In order



to understand the taxonomic history of *Sarcostemma*, it is essential to recognize that there are two main problems involved. First, there is the misapplication of several generic names and the consequent confusion in their usage up to the present day. Second, there is the question of how many segregates can be maintained without endangering the integrity of the genus as a practical unit.

*Sarcostemma* was described by Robert Brown<sup>1</sup> in 1809 in his classic paper on the separation of the Apocynaceae and Asclepiadaceae. The only species known to him at that time were succulent lianas of Asia and Africa having the leaves reduced to scales. They were characterized by rotate flowers provided with a pronounced faucal annulus or outer corona, and an inner corona consisting of five separate, inflated lobes (to which the name alludes). Ten years later, Kunth<sup>2</sup> described, as species of *Sarcostemma*, a series of American forms of similar floral structure, but with laminate leaves. For a species having the corolla campanulate, he inaugurated the new genus *Philibertia* HBK. He also noted that the outer corona in *Philibertia* was less prominent than in *Sarcostemma*.

In his account of the Asclepiadaceae for the 'Prodromus' of De Candolle, Decaisne<sup>3</sup> recognized only the genus *Sarcostemma*, which consisted, however, of two sections: EUSARCOSTEMMA and PHILIBERTIA. The former included both New World and Old World forms with rotate corollas, while the latter contained only New World species with "*corolla urceolato-rotata*." Decaisne himself described most of the American species of both EUSARCOSTEMMA and PHILIBERTIA included in his account.

The peculiar confusion in the taxonomy of the genus began in 1876 when Bentham<sup>4</sup> referred all of the New World species to the genus *Philibertia* HBK., regardless of the shape of the corolla. Shortly thereafter, Gray<sup>5</sup> and Hemsley<sup>6</sup> made the necessary new combinations for species of the United States and Latin America. Fournier<sup>7</sup>, on the other hand, in the 'Flora Brasiliensis', followed Decaisne in the use of *Sarcostemma* for rotate-flowered species, although he had to deal with no species of *Philibertia* (*sensu* HBK.).

In the preparation of his treatment of the Asclepiadaceae for Martius' great work, Fournier apparently made a careful study of the Latin American species. It is interesting to note that a tendency to draw taxonomic lines rather finely was emphasized in his establishment of the genera *Funastrum*<sup>8</sup> and *Cystostemma*<sup>9</sup>. Of the two species included within *Funastrum* by Fournier, only one is referable to *Sarcostemma*, this being *F. angustissimum* (Anderss.) Fourn. of the Galapagos Islands. The other is an Argentine species of *Cynanchum* (*Ditassa*). *Cystostemma* was erected for a species which completely lacks the faucal annulus or ring of the corona; in all other respects it is so close to the other New World sarcostemmas

<sup>1</sup>R. Brown, in Mem. Wern. Soc. 1:50. 1809.

<sup>2</sup>Kunth, in HBK. Nov. Gen. et Sp. Pl. 3:195. 1819.

<sup>3</sup>Decaisne, in DC. Prodr. 8:537. 1844.

<sup>4</sup>Bentham, in Benth. & Hook. Gen. Pl. 2:733. 1876.

<sup>5</sup>Gray, in Proc. Amer. Acad. 12:64-65. 1877.

<sup>6</sup>Hemsley, in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:320. 1881.

<sup>7</sup>Fournier, in Mart. Fl. Brasil. 6<sup>4</sup>:233-235. 1885.

<sup>8</sup>Fournier, in Ann. Sci. Nat. Bot. VI, 14:388. 1882.

<sup>9</sup>Fournier, in Mart. loc. cit. 204. 1885.



that nearly all subsequent authorities are in agreement as to its conjunction with that group of species. Both *Funastrum angustissimum* (Anderss.) Fourn. and *Cystostemma umbellatum* Fourn. are here made the bases for monotypic series of subg. CERAMANTHUS.

The most recent treatment of Asclepiadaceae as a whole is that of K. Schumann<sup>10</sup> in 'Die Natürlichen Pflanzenfamilien'. The rather generally unsatisfactory aspects of his system are well-exemplified by his handling of the *Sarcostemma* problem. The American species with campanulate flowers were transferred to the Old World genus *Oxystelma* R. Br., leaving in *Philibertia* only those forms with rotate corollas, while *Sarcostemma* was limited to the Old World forms with scale-like leaves. *Oxystelma* and *Philibertia* were placed in the same subtribe (GLOSSONEMATINAE), while *Sarcostemma* and the synonymous genus *Funastrum* were put into different subtribes (CYNANCHINAE and ASCLEPIADINAE, respectively).

Realizing that the species then included in *Philibertia* did not accord with the original description of the genus, Miss Vail<sup>11</sup> proposed for them the new name *Philibertella*. She concurred with Schumann in the disposition of the campanulate-flowered species. However well-meant her intentions, the name only added to the confusion, for it took its place with *Sarcostemma*, *Philibertia*, and *Oxystelma*, all being used for the same species.

The Swedish asclepiadologist Malme<sup>12</sup> also attempted to rectify the error of Schumann by elevating the subgenus CERAMANTHUS Kunze<sup>13</sup> to the rank of genus. But he cited as synonyms, *Funastrum*, *Cystostemma*, and *Philibertella*. It is difficult to understand why Malme chose *Ceramanthus* when several names of generic rank were available; moreover, the name is antedated by *Ceramanthus* Hassk.<sup>14</sup> and *Keramanthus* Hook. f.<sup>15</sup> Fortunately it never was used as widely as were the other current names.

Schlechter<sup>16</sup>, in a critical discussion published in 1915, came to the conclusion that the group of rotate-flowered species of the New World was sufficiently distinct to be designated as a genus and he made the requisite combinations in *Funastrum*. At the same time he reinstated *Philibertia* for the campanulate-flowered species.

Most recently, Woodson<sup>17</sup> has returned to the system of Decaisne, uniting *Funastrum* and *Philibertia* with the Old World forms under the name *Sarcostemma*. Redintegration appears to be the only satisfactory way of solving the problem, for the three groups of species are very close, and characters formerly used to separate them are found to break down when all of the species are studied together. It is the course followed in this paper, where the three groups of species constitute sub-

<sup>10</sup>Schumann, in Engl. & Prantl, Natur. Pflanzenfam. 4<sup>2</sup>:189-306. 1895.

<sup>11</sup>Vail, in Bull. Torr. Bot. Club 24:305-311. 1897.

<sup>12</sup>Malme, in Arkiv Bot. 4<sup>14</sup>:2. 1905.

<sup>13</sup>Kunze, in Linnaea 20:26. 1847.

<sup>14</sup>Hasskarl, in Cat. Hort. Bogor. Alt. 240. 1844.

<sup>15</sup>Hooker f. in Curt. Bot. Mag. t. 6271. 1876.

<sup>16</sup>Schlechter, in Fedde's Repert. 13:279-287. 1915.

<sup>17</sup>Woodson, in Ann. Mo. Bot. Gard. 28:193-244. 1941.



genera: *EUSARCOSTEMMA*, *CERAMANTHUS*, and *OXYSTELMA*. When once this step is taken, however, a serious question of generic limits arises. If *Sarcostemma* is to be defined as a stable entity, a number of closely related genera must be placed in synonymy.

As even Schumann realized, the Old World *Oxystelma* R. Br.<sup>18</sup> is very close to *Philibertia* HBK., agreeing in such points as the campanulate corolla and the ring of the corona adnate to the corolla-tube. *Oxystelma* is here reduced to the rank of a subgenus of *Sarcostemma*, and it includes the species formerly assigned to *Philibertia*.

The genus *Pergularia* L.,<sup>19</sup> of Africa and Asia, superficially appears similar to *Sarcostemma* in that the corona consists of five inflated lobes and a porrect ring which is free from the corolla. There are numerous points of difference, however, which I summarize in the following table:

<i>Sarcostemma</i>	<i>Pergularia</i>
Corolla rotate-subcampanulate, salverform with an inconspicuous tube, or campanulate	Corolla salverform with a conspicuous tube.
Ring of the corona thick and short, entire.	Ring of the corona thin and relatively long, 5-lobed, and denticulate.
Vesicles of the corona obtuse to acute, very rarely attenuate, never spurred.	Vesicles of the corona long and attenuate, spurred.
Pollinium-sac essentially uniformly fertile, the corpusculum radially compressed.	Pollinium-sac with a narrow, hyaline, outer margin, the corpusculum strongly compressed tangentially.
Follicles glabrous to pubescent.	Follicles rather copiously puberulent, usually echinate.

In view of these differences, especially of the pollinium, it would seem best to maintain *Pergularia* as a separate genus. Decidedly it does not seem advisable to complicate further the synonymy of the sarcostemmas by changing them all to *Pergularia*.

There are a number of other genera which have been put into the synonymy of *Philibertia* HBK. and *Funastrum* Fourn., and these must now be regarded as synonymous with *Sarcostemma*. Such are *Pentagonium* Schauer<sup>20</sup> and *Zosima* Philippi<sup>21</sup>, monotypic genera, both of which apply to species of the subgenus *OXYSTELMA*; the latter is a later homonym of *Zosima* Hoffm.<sup>22</sup> Similarly, *Lugonia* Wedd.<sup>23</sup> was described on the basis of an Andean plant which represents nothing more than an alpine modification, and which is referred also to subg. *OXYSTELMA*.

Rather perplexing are *Pentacyphus* Schltr.<sup>24</sup> and the very similar *Tetraphysa*

<sup>18</sup>R. Brown, in Mem. Wern. Soc. 1:40. 1809.

<sup>19</sup>Linn. Mantissa, p. 8. 1767 (not of other authors), cf. N. E. Brown in Kew Bull. 1907:323, who shows that *Doemia* R. Br. is the same as the Linnean *Pergularia*.

<sup>20</sup>Schauer, in Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1:364. 1843.

<sup>21</sup>Philippi, Sert. Mend. Alt. 29. 1871.

<sup>22</sup>Hoffman, Gen. Umbell. 145, t. 4. 1814.

<sup>23</sup>Weddell, Chloris Andina 2:49. 1857.

<sup>24</sup>Schlechter, in Engl. Bot. Jahrb. 37:605. 1906.



Schltr.<sup>25</sup> While they diverge considerably from *Sarcostemma* as exemplified by the type species, the former is sufficiently close to species of subg. OXYSTELMA to be considered a separate section of subg. OXYSTELMA, and *Tetraphysa* inevitably follows it.

The following synopsis, then, summarizes the structure of the genus as I view it; and in it I take the opportunity to describe a new section and to make several nomenclatural adjustments for Old World forms which will not be discussed further taxonomically.

Subg. CERAMANTHUS	{	.....Ser. PANNOSA.....	<i>S. pannosum</i>	
		.....Ser. CLAUSA.....	{ <i>S. glaucum</i> <i>S. clausum</i>	
		.....Ser. CYNANCHOIDES.....	{ <i>S. bilobum</i> <i>S. odoratum</i> <i>S. gracile</i> <i>S. crispum</i> <i>S. elegans</i> <i>S. Torreyi</i> <i>S. cynanchoides</i> <i>S. birtellum</i> <i>S. arenarium</i>	
		.....Ser. ANGUSTISSIMA.....		<i>S. angustissimum</i>
.....Ser. FLAVA.....	<i>S. flavum</i>			
Subg. OXYSTELMA	{	Sect. PHILIBERTIA.....	{ <i>S. campanulatum</i> <i>S. Gilliesii</i> <i>S. albiflorum</i> <i>S. solanoides</i> <i>S. stipitatum</i> <i>S. lysimachioides</i>	
		Sect. PENTACYPHUS.....		{ <i>S. andinum</i> <i>S. Lehmannii</i>
		Sect. EUOXYSTELMA <sup>26</sup> .....		<i>S. esculentum</i> <sup>27</sup>
Subg. EUSARCOSTEMMA <sup>28</sup>			(several species)	

<sup>25</sup> Schlechter, loc. cit. 616. 1906.

<sup>26</sup> *Euoxystelma* R. Holm, sect. nov.: coronae squamae ovoidae apice caudatae incurvatae gynostegium superantes, coronae annulus et columna pubescentes; caudiculae obsoletae. T.: *Sarcostemma esculentum* (L.f.) R. Holm.

<sup>27</sup> *SARCOSTEMMA esculentum* (L.f.) R. Holm, comb. nov. *Periploca esculenta* L.f. Suppl. 168. 1781.

<sup>28</sup> Subg. *Eusarcostemma* (Decne.) R. Holm, stat. nov. Sect. *Eusarcostemma* Decne. in DC. Prodr. 8:538. 1844.



## MORPHOLOGY

All the species of *Sarcostemma* are suffrutescent, dextrorsely twining or trailing vines. In the tropics they may climb high into trees and shrubs, but in alpine or desert areas they are reduced to semi-erect or prostrate subshrubs, variously woody or succulent.

The primary root generally is slightly thickened, forming a slender tap-root. Aerial adventitious roots have been noted in several plants which had been growing in very moist habitats; apparently they are never produced on climbing stems, and but rarely on trailing shoots.

The stems of all the species are more or less woody below and herbaceous above. In temperate latitudes, the plant dies back to this woody base during the winter or dry season. If environmental conditions are harsh, the herbaceous stems may be greatly reduced and either semi-erect or prostrate; or, as in subg. *EUSARCOSTEMMA*, succulent, with the leaves reduced to scales. The plants usually are twining vines, extending from one to more than thirty meters into trees and shrubs.

The woody basal portion of the stem is covered with the ridged, yellow bark of loose texture which is more or less characteristic of the *Asclepiadaceae*. This bark is first produced at the nodes where there may be corky knobs or ridges decurrent upon the internodes. Above these first few centimeters, the stem is gray- or yellow-green and may be pubescent or glabrous. Even in the latter case, there is usually much pubescence in the axil of the leaves and on the buds. In some species, the young stems are extremely pubescent, becoming less so at maturity.

The number of lateral branches normally produced is variable, but is a good character for several groups of species. When the plant branches profusely, the lateral branches usually are intertwined with each other and the main stem. There seems to be little correlation between the amount of branching and the type of habitat, although plants growing in the open tend to be more branched.

The leaves in *Sarcostemma* are entire and opposite and, on the monopodial portion of the stem, they are strictly decussate. After an inflorescence has been produced, the stem becomes sympodial (*vide infra*) and the leaves of each sympodium member no longer are at right angles to those at the floriferous node next below. By far the majority of the species have cordate leaves with characteristic palmate or pedate venation. As a rule, leaf shape can be used to distinguish groups of species, but there is much variation in the length/width ratio. In the desert species of *EUSARCOSTEMMA*, the leaves are reduced to scales which sometimes are difficult to find, for they wither rapidly. In this connection, it is interesting to note that in *S. clausum*, and less frequently in *S. glaucum* (subg. *CERAMANTHUS*), of the dry, coastal habitats of western Peru and Colombia, the leaves often are much reduced in size. In these species, as well as in *S. cynanchoides* ssp. *Hartwegii* (of the same subgenus, but occurring in arid, southwestern United States), the leaves sometimes are caducous, the aspect of the plant then being superficially much like that of a slender *S. viminale* (*EUSARCOSTEMMA*).



Most commonly, the margins of the leaves are entire and somewhat revolute, but they are undulate in several species of two subgenera. This condition apparently is caused by the continued proliferation of the lateral meristems of the leaf after interstitial growth has ceased, and is quite variable in intensity. In *S. crispum*, strikingly undulate leaves are the rule in Texas, but the degree of crisping is much less to the south and west where there actually may be no sign of it. Greenhouse plants of *S. pannosum*, which has less pronounced crisping, may have distinctly undulate and quite plane leaves upon the same shoot.

In nearly every specimen, one finds at the base of the leaf on the ventral surface of the point of juncture of the main veins, a number of small, digitiform structures referred to as "glands" in the taxonomic literature (fig. 1). They are yellow or orange in color and vary in size with the vigor of the plant. In desert

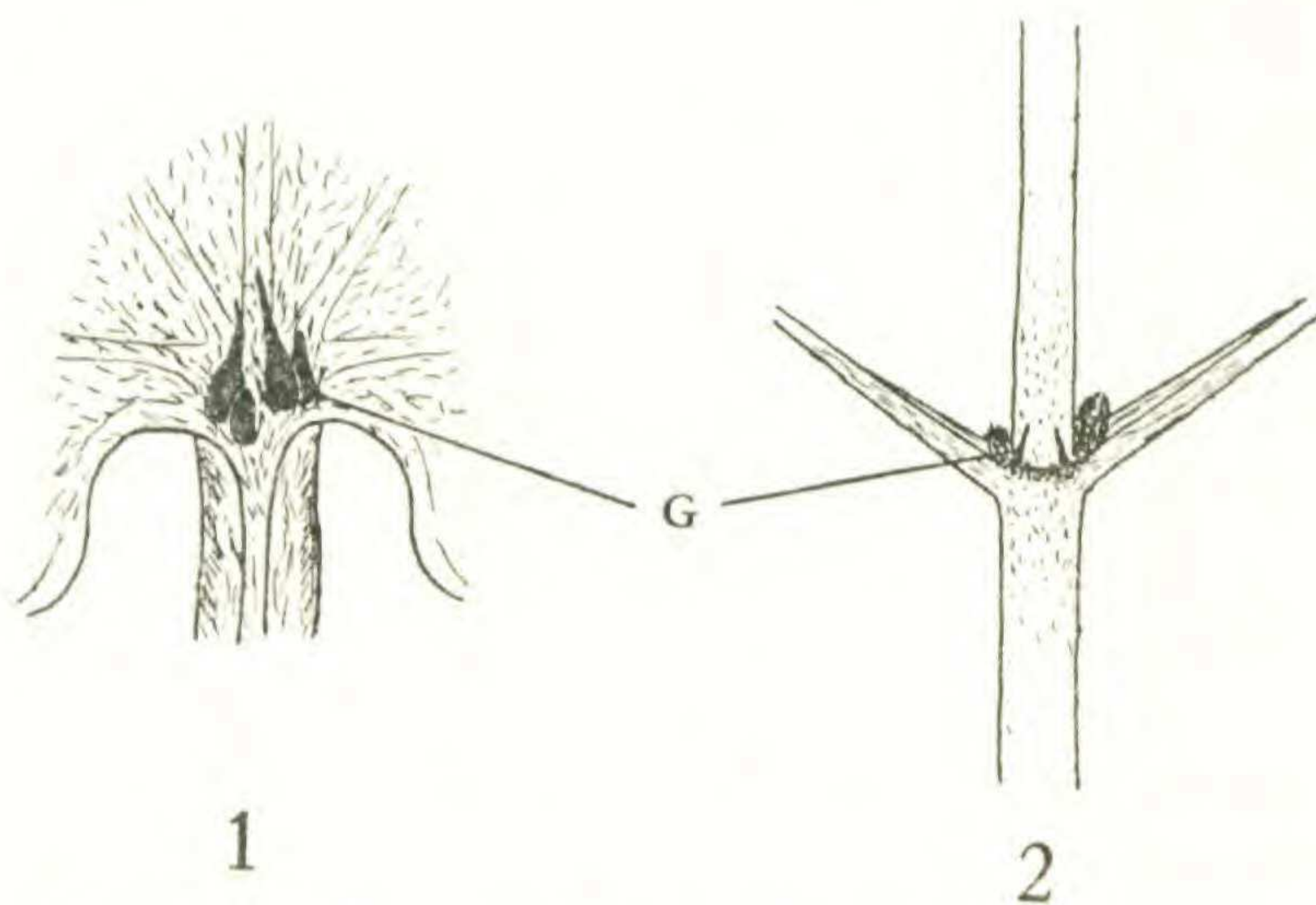


Fig. 1. Foliar glands: 1, base of blade; 2, node; G, gland.

species they usually are reduced in size or occasionally absent. Similar "glandular" structures are found at the nodes, lateral to the petioles, where their position and arrangement suggest that they are reduced stipules; this view is further supported by the fact that occasionally they are slightly laminate. The foliar "glands" are of no taxonomic significance, and their morphological or physiological importance is uncertain. As in the Apocynaceae, the petioles are connected by an interpetiolar ring which appears as a fleshy excrescence of the subjacent internode (fig. 1). The petiolar "glands" are inserted upon the edge of this ring, which also may be puberulent, especially adjacent to the petioles. When the stipular appendages are lacking, there often are tufts of hairs in a corresponding position.

There now can be little doubt that the inflorescence in the Asclepiadaceae is basically terminal, despite the considerable controversy which has taken place in the past. Anatomical, morphological, and experimental studies<sup>29</sup> are fairly clear

<sup>29</sup>cf. Demeter, in *Flora* 115:130-176. 1922; and Schoute, in *Rec. trav. bot. Neerl.* 34:182-204. 1937, each with a comprehensive bibliography.



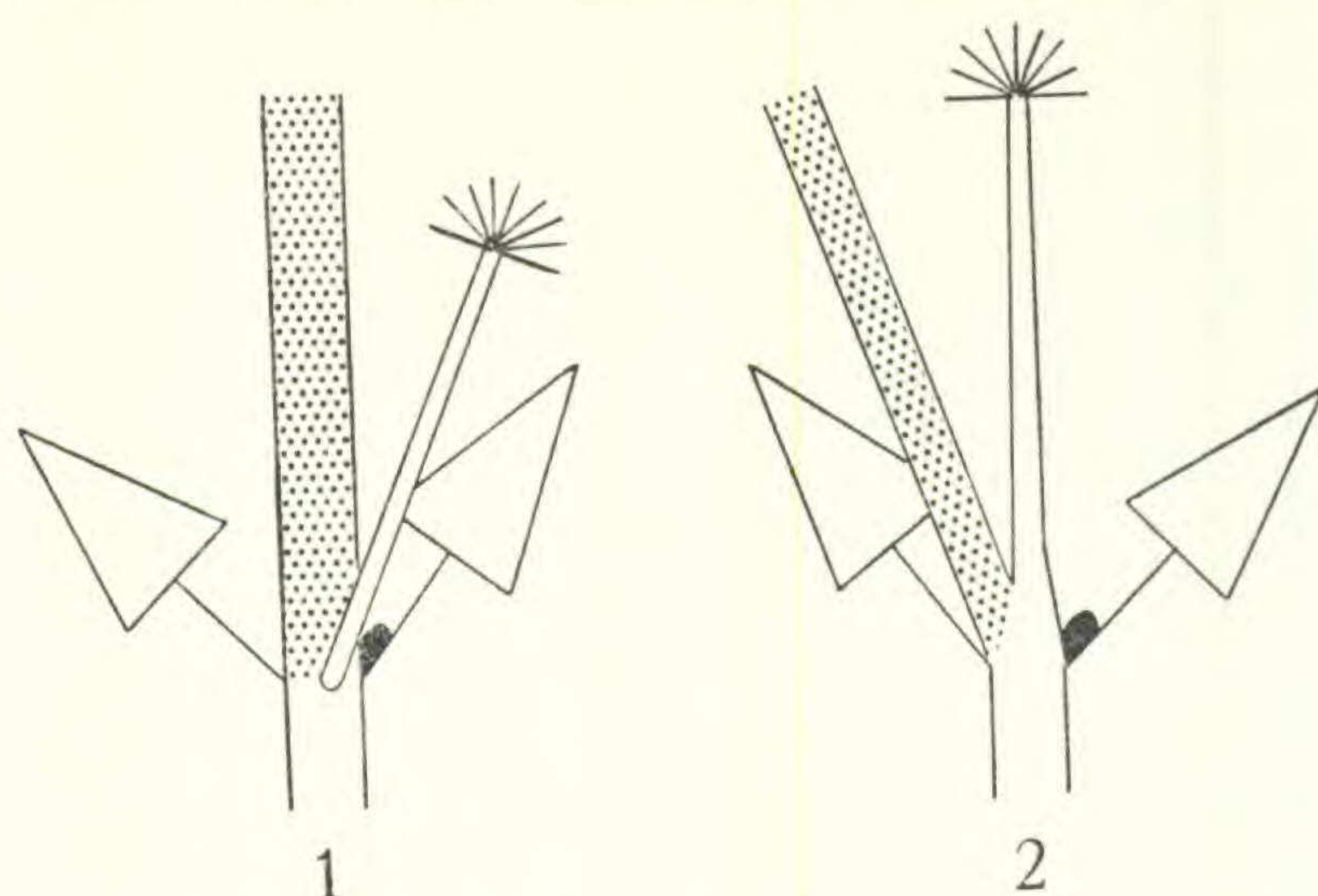


Fig. 2. Diagrams of inflorescence-bearing nodes: 1, actual appearance; 2, morphological interpretation; shading indicates axillary growth.

on this point. The axis which continues the growth of the plant after the first inflorescence arises from one of the buds of the last vegetative node, as is diagrammed in fig. 2. According to the unfortunately highly formalized interpretation of Schoute<sup>30</sup>, subsequent sympodium members arise from the axils of the  $\beta$ -prophylls. This is only another way of stating that, with continued inflorescence production, each succeeding internode arises from one of the first two, opposite, leaves ("prophylls") of the node next below; there are, of course, no more than two leaves on this shoot.

Inspection of a vegetative shoot of *Sarcostemma* (fig. 3) shows that the buds in the axils of the paired leaves differ markedly in size; in fact one may be absent altogether. This is the rule in the Asclepiadaceae. If we consider the small buds and large buds separately, we find that they form two opposed spirals with  $90^\circ$  divergence. The first inflorescence terminates this monopodial axis, but is pushed aside by the vigorous growth of the large bud of the last leaf-pair. This shoot forms the first sympodium member, as the upper portion of fig. 3 indicates. The small bud in the axil of the other leaf sometimes grows, but rarely equals the main shoot. The reproductive phase, once initiated, continues indefinitely, each sympodium member bearing two leaves and an inflorescence. The rectangular crossing of the leaves is replaced then by a skew-crossing, for two of the angles between rows of leaves are obtuse and two are acute. As a result, the inflorescences, which are interpetiolar but nearest the large bud of the associated pair of leaves, are borne in two nearly straight rows on opposite sides of the stem, diverging from one another at  $150-180^\circ$ . The bud near the inflorescence is, of course, that which formerly was denoted as a "small" bud, for the large bud has become a sympodium member. A disturbing feature is the presence of an additional bud in the axil of the leaf which presumably subtends the main axis. This bud, which Schoute<sup>31</sup> dismisses as a "small accessory bud," I take to be of the nature of those which are present in such genera as *Juglans*, and which also have been reported for the

<sup>30</sup>Schoute, loc. cit. 1937.

<sup>31</sup>Schoute, loc. cit. p. 187. 1937.



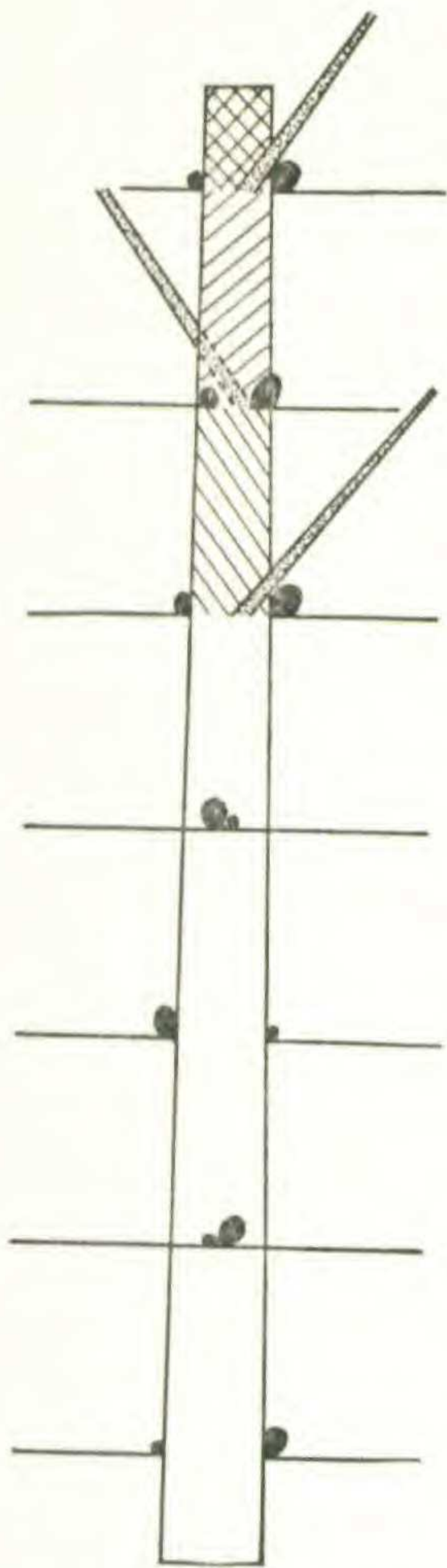


Fig. 3. Diagram of portion of stem of *Sarcostemma* showing large buds and small buds and arrangement of the inflorescences; shading indicates successive internodes of axillary growth.

Apocynaceae. In *Sarcostemma*, the presence or absence of the accessory bud varies both between and within species. Its absence appears to be correlated with a desert or open habitat.

Should the vegetative phase be resumed after a period of inflorescence production, the axis again becomes monopodial and the leaves strictly decussate. It is hardly necessary to add that the torsions introduced by the voluble habit greatly obscure the details of inflorescence and leaf arrangement which are sufficiently difficult to follow on the stem of erect forms.

This condition of the inflorescence is a general one throughout the Asclepiadaceae, and may be noted even in such modified forms as *Stapelia*. In those genera where the inflorescence appears to be axillary, it may be interpreted as terminal according to Schoute. Very rarely, as in *Sarcostemma angustissimum*, the inflorescence actually is terminal to the main axis or a lateral branch. Only one floriferous lateral branch is produced at a node in the latter case. It appears plausible to consider this a case of reduction and specialization, rather than one of primitiveness.

The type of inflorescence is quite variable in *Sarcostemma*. Usually it is umbelliform in subg. CERAMANTHUS and racemiform in EUSARCOSTEMMA and OXYSTELMA. The basically cymose nature of the inflorescence is demonstrated by the irregularly centripetal development of the flowers and by the arrangement of the flowers upon the floriferous axis.

In the subg. CERAMANTHUS, the type of inflorescence has been used to distinguish four series. *Sarcostemma pannosum* is placed in a series by itself since the inflorescence always is manifestly compound. The nodeless peduncle may dichotomize in extreme cases producing two cincinni, each more than a centimeter in length. Upon the axis the flowers are disposed spirally in pairs.

A second series includes *S. clausum* and *S. glaucum* in which the peduncle ordinarily equals or exceeds in thickness the axis below the inflorescence-bearing node. Frequently it bears two catenulate cymes; the inflorescence is umbelliform, all the flowers appearing to come from about the same place, but blooming in an irregularly centripetal fashion. The second cyme, if present, is lateral and sessile upon the peduncle.



Most of the species of subg. CERAMANTHUS fall into a third series in which the inflorescence is umbelliform and is borne upon a slender peduncle which only very rarely equals the stem in thickness or bears a secondary cyme. *Sarcostemma angustissimum* is placed in a monotypic series on the basis of its terminal inflorescence; the peduncle is short or absent, but when present is not equal to the stem in thickness.

The inflorescence in subg. OXYSTELMA most commonly is racemiform, although the superficial appearance of occasional individual plants may belie their structure. Thus while all of the species with racemiform structure may experience such abbreviation of the floriferous axis as to simulate the umbelliform type in one or more inflorescences, comparison of a number of inflorescences, or careful examination of the peduncle for bracts, will reveal the racemiform nature. On the other hand, *Sarcostemma solanoides* presumably never deviates from the strictly umbelliform inflorescence. *Sarcostemma* (§ PENTACYPHUS) *andinum* apparently illustrates reduction from the racemiform type along different lines: invariably there are two nodes in the inflorescence, each of which bears a single flower. Again it must be realized, however, that specimens of species with typically racemiform inflorescences (which have the flowers arranged in pairs along an axis of several nodes) may assume this appearance. The nature of the inflorescence has not been used to delimit series in OXYSTELMA since the species do not seem to fall into natural groups along these lines.

In all the species of *Sarcostemma*, there is a tendency for a more or less specialized reproductive portion of the axis to be developed. This condition is most clearly seen in *S. clausum* and *S. glaucum* where the inflorescences may be borne upon long, lateral branches which have reduced leaves, the whole resembling the compound inflorescences of certain species of *Cynanchum* (*Tassadia*).

Length of the peduncle is a character which has been used with disastrous results in the past, as a glance at the synonymy of *S. clausum* will testify. Many of the segregates of that species were based upon slight differences in the length of the peduncle relative to the associated leaves. Within several species the peduncle may be much longer than the leaves or absent entirely. In certain species, however, the extreme conditions are valid characters, e. g. in *S. elegans* vs. *S. Torreyi*.

Few distinctive features are presented by the pedicels. Relative number, thickness, and length are of some value in setting apart groups of species, but have little practical use. The pedicels elongate gradually until anthesis, and if fertilization takes place and a fruit is formed, the pedicel and peduncle enlarge to support the follicle.

The calyx in *Sarcostemma* is gamosepalous, and the lobes are divided nearly to the base. The upper surface usually is glabrous, but the lower varies from glabrous to densely pubescent. In many cases, especially in subg. CERAMANTHUS, the marginal hairs are long, making the lobe ciliolate. Within the calyx tube, generally distributed about the base or alternating with the lobes, are one or more digitiform



structures commonly called "glands." These apparently are homologous with the calycine squamellae of the Apocynaceae which have been interpreted as being of stipular origin<sup>32</sup>. In the apocynaceous genera studied, they were correlated with the nature and arrangement of the stipules and were constant within a genus or subgenus. No such correlations have been noted in *Sarcostemma*; the number and distribution of the squamellae are variable and without taxonomic significance. A squamella consists of a central core containing many druses and an outer, deeply-staining, palisade epidermis.

It would appear that where reduction in size of certain structures has proceeded to a given point, they assume this more or less cylindrical, translucent, lutescent appearance of the "glands." This may be noted, for example, for the stipules. Occasional aberrancies also are suggestive: in one specimen of *S. clausum*, a single calyx lobe had a "glandular," lateral appendage at the base; in *S. angustissimum*, the minute calyx lobes are "glandular" at the apex; in *S. lysimachioides*, the squamellae are borne in groups at the margin of a triangular pad of tissue alternating with the calyx lobes; finally, in those species with mucronate leaves, the mucro often is strikingly similar to the various "glands" in appearance. On the other hand, there is some indication that the multicellular hairs found upon the interpetiolar ring and the calyx lobes may become "glandular" in appearance. The whole problem is one which would repay investigation, for upon its solution depends our interpretation of the calycine squamellae and the appendages of the leaves.

The corolla is gamopetalous, and the degree of cohesion of the lobes is an important taxonomic character. In general, species of subg. OXYSTELMA have very broadly campanulate corollas which are shallowly lobed; in the angles of the sinuses there often are minute petalaceous teeth. The corolla in subg. CERAMANTHUS and EUSARCOSTEMMA is rotate-subcampanulate or salverform and is divided nearly to the gynostegium. The corolla lobes usually are spreading or ascending, but they may be strongly reflexed.

It is the behavior of the androecium and gynoecium which characterizes the Asclepiadaceae as a family, hence it will not be amiss to describe in some detail the morphology and anatomy of the structures in these two floral whorls. The material on which the following discussion is based consists of longitudinal and cross sections of flowers and buds; extensive use also has been made of flowers and buds cleared in 5 per cent sodium hydroxide solution and treated with lactic acid. The latter technique is especially useful, for the sodium hydroxide removes all coloring material from the tissues rendering them transparent; the cell walls, however, are undistorted and may be studied with or without the application of a stain.<sup>33</sup> In such preparations, the course of the vascular bundles may be followed *in situ* and a clearer concept of the spatial relations of the various parts may be obtained without the laborious method of reconstructing from a series of sections.

<sup>32</sup> Woodson, R. E., and Moore, J. A., in Bull. Torr. Bot. Club 65:135-166. 1938.

<sup>33</sup> This technique is described in A. S. Foster's 'Practical Plant Anatomy,' 1949. Staining is discussed by Thomas Morley in Stain Techn. 24:231-235. 1949.



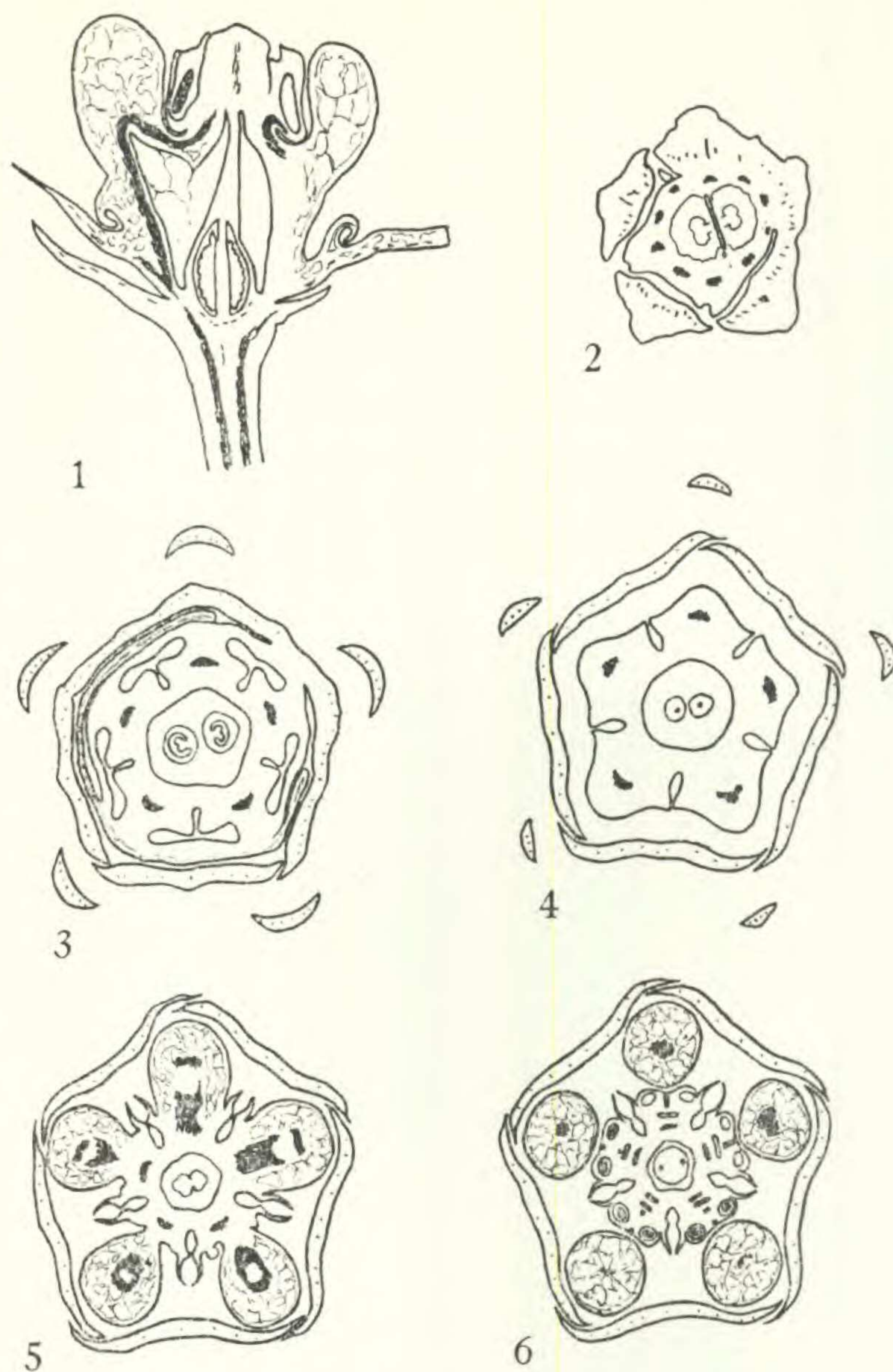


Fig. 4. Longitudinal section of flower and cross section of bud: 1, longitudinal section of flower showing vascular bundle of stamen, ring of the corona, and slightly immersed carpels; 2, cross section through receptacle showing sepals, squamellae, and carpels immersed in the receptacle; 3, cross section through the region of the corona ring showing ring, corolla, and the staminal column; 4, cross section through the staminal column showing grooves and the styles; 5, cross section through the region of the corona vesicles showing vascular bundle in the corona vesicles and the anther-wings; 6, cross section through the gynostegium above the attachment of the corona vesicles showing the thecae and pollinium-sacs, anther-wings, and the base of the stigma-head.

Supplementing the description which follows are the semi-diagrammatic drawings of fig. 4 which represent cross sections of a bud, and a longitudinal section of a flower of *Sarcostemma pannosum*. The five antesepalous stamens are borne upon the corolla tube near the base and are coherent laterally almost to their apices, forming an epipetalous tube. The united filaments constitute what commonly is called the column. Externally, the filaments are marked by deep grooves in the



column in subg. CERAMANTHUS and EUSARCOSTEMMA, but these usually are lacking in OXYSTELMA. In *S. andinum*, the margins of the groove are extended at an angle of about  $45^{\circ}$  to the column, forming two prominent flaps continuous with the anther-wings.

The anthers contain but two pollen-sacs, each of which is visible dorsally as an elongate protuberance. The connective is prolonged into a short spike which supports a membranous margin. This apical appendage of the anther usually is appressed to the stigma-head. Ventrally, the anthers are coherent by their margins except for a short distance at the apex. The five sinuses thus produced in the staminal tube expose the receptive surface of the stigma, as will be discussed below. Laterally also, but abaxial, the margins of the anthers are produced to form the anther-wings or anther-alae. These are continuous with the margins of the groove in the column from which they differ markedly, however. Histologically, the transition is marked by a change in the composition of the cell walls as is indicated by their greater affinity for basic dyes (e. g. safranin).

Morphologically, the anther-wings are characterized by their cartilaginous texture and appearance, and by the fact that they are produced somewhat beyond the margins of the groove in the column. They are inclined at an angle of about  $45^{\circ}$  to the plane of the thecae and are recurved so that their edges are closely appressed. Towards the base there is an opening into the so-called alar chamber delimited ventrally by the conjoined anthers and laterally by the anther-wings. This orifice varies in size and shape from thin and narrow to large and circular. It is the opening into which the instrument of pollination is introduced.

As in all Cynanchoideae, the stamens at maturity are closely connivent with the united styler region of the carpels (referred to as the stigma-head). While it is stated commonly that the anthers are merely loosely connivent with the stigma-head or united only by their tips, neither of these descriptions is accurate. The young anthers are at first free from the gynoecium. Fairly early in their development, however, the ventral surface of the staminal tube bulges to form a pronounced flange about the circumference of the staminal tube at the level of the locules. This flange in later development becomes closely appressed to the lower surface of the stigma-head and the tissue of the two structures finally becomes joined. It can be seen in sections of the flower that the cells of one dovetail between those of the other and that there is a slight crushing and disruption of the superficial layers. In this area, the highly differentiated, columnar epidermis of the stigma-head is unchanged in the bud stage, but by the time of anthesis, the cells have lost their characteristic rectanguloid shape and their strong affinity for stains. The anthers are free from the stigma-head around its entire circumference except at the flange. The lateral surface of the stigma is exposed, however, only at the five sinuses in the staminal tube, which are hidden within the alar chambers.



We come now to those structures of the androecium which collectively make up the corona. Woodson<sup>34</sup> has pointed out the dangers of lack of precision in the use of the word corona, which he rightly applies to "various elaborations or enations of the staminal filaments only." That definition is followed in this paper for the reason that there are at least three structures which have been, or could be, interpreted as corona in *Sarcostemma*. It is customary to speak of inner and outer corona, but there is no assurance that the "inner corona" of one group is not the equivalent of the "outer corona" of another, nor that it will not be mistaken for such by the user of the, at first sight, obvious key character. In many genera of the Asclepiadaceae, there are three appendages of the stamens, as well as others of the corolla, so that any distinction of "inner" or "outer" corona becomes impossible.

In nearly all the species of *Sarcostemma*, there is a so-called "outer corona" or "faucal annulus." Whether this structure pertains to the corolla or to the androecium is not easy to determine; indeed, I am not certain what evidence could be considered definitive in the light of recent studies of the development and initiation of floral parts. The ring of the corona is best studied in the species of the subgenera CERAMANTHUS and EUSARCOSTEMMA, where it reaches maximum development. In subg. OXYSTELMA, the ring is present but usually abbreviated or adnate to the corolla. The corona ring may be a ridge at the base of the staminal column or a thick, revolute fold of tissue free from the corolla except at the very base. In many species, the ring is adnate to the androecium directly below the anthers; in others it is adnate to the corolla; finally, there are species in which the ring is adnate both to androecium and corolla. Cross and longitudinal sections show that the ring is more or less double at maturity and is composed of the same type of rather loose parenchyma as are the corolla and corona vesicles borne upon the filaments. No vascular supply is present, nor does the staminal trace diverge from its course in the direction of the ring. Viewed superficially, the corona ring is similar in texture to the androecium and not to the corolla. In subg. OXYSTELMA, § EUOXYSTELMA, both the column and corona ring are often puberulent, while the corolla is glabrous.

In the hope that developmental studies might shed some light on the problem, sections of buds and buds of varying age, cleared with sodium hydroxide, were examined. The later development of the flower studied here is remarkably similar to that described by Boke<sup>35</sup> for *Lochnera rosea*. As in that species, it is possible to distinguish two portions of the corolla tube: that below the insertion of the stamens, and that above this point. The lower corolla tube in *Sarcostemma* appears to be of receptacular origin, as is the case in *Lochnera*. The corolline traces do not branch until they reach the point of staminal insertion, whereupon two laterals depart simultaneously from each, run periclinally to the margins of the lobe, finally

<sup>34</sup>Woodson, in Ann. Mo. Bot. Gard. 28:199. 1941.

<sup>35</sup>Boke, Norman H. A series of three papers in Am. Jour. Bot. 34:433-439; 35:413-423; 36:535-547. 1947-1949.



to pursue their customary course upwards. A number of secondary branches from the distal margin of the horizontal portion of the laterals supply most of the mesophyll of the corolla lobe. Distal to the androecium, the upper corolla tube appears to be the result of ontogenetic fusion of separate lobes. The two lateral veins are closely appressed and traces of former epidermal layers often can be made out, especially near the sinus. The proximal portion of the upper corolla tube is slightly thickened by an adaxial meristem of the sort noted by Boke.

Unfortunately, the origin of the corona ring is not clarified by a study of development because of its early association with both the upper corolla tube and the staminal column. As nearly as I can determine, it arises in the angle of the sinus formed by the insertion of the stamens upon the corolla. Opposite a stamen, the ring appears first as a protuberance from the column; opposite a corolla lobe it appears in the sinus (in the bud stage).

Though the evidence is by no means clear-cut from this preliminary work, I am of the opinion that the corona ring must be considered a part of the androecium if we are to attempt to assign such structures to one of the formal categories of descriptive morphology. Comparison of *Sarcostemma* with a number of other forms in the Cynanchoideae shows that many have a tendency, expressed to a greater or lesser extent, for the base of the staminal tube to flare out into a corona ring, e. g. *Fischeria*, *Gonolobus*, and other genera, especially of the Gonolobeae. Perhaps the corolline faucal annuli of such forms as *Stapelia* and *Periploca* are the result of growth of the adaxial or ventral meristem discussed by Boke and Troll.

The so-called "inner corona" is composed of five vesicular outgrowths of the filaments directly below the anthers. Since the corona, as I interpret it, comprises both the ring at the base of the column and these enations of the filaments contiguous to the anthers, I shall refer to its components as corona ring and corona vesicles. The vesicles are constituted of a loose parenchyma which becomes distorted during later growth. They arise late in ontogeny so that in a bud, even shortly before anthesis, they may be quite small. Incidentally, this has led to the description, in other genera, of species "*parvicoronata*," etc. based on nearly mature buds. Towards the base of the vesicle, the staminal trace usually arcs strongly upwards into the corona segment before reaching the anther.

The corona vesicles arise as small protuberances increasing in size gradually by interstitial growth, for the most part. Shortly before anthesis, rapid growth ensues, principally in the epidermal and immediately subjacent layers. The deeper-lying cells are stretched to form an aerenchyma and may be grotesquely twisted. Probably it is the inclusion of innumerable intercellular spaces filled with air which gives to the vesicles their characteristic, almost crystalline, appearance.

The corona vesicles are quite variable in shape. At the opening of the flower they are ovoid or obovoid, occasionally somewhat quadranguloid or laterally compressed. The upper end is rounded, truncate, or pointed; frequently there is an apiculation on the inner side at the apex. In subg. *OXYSTELMA* § *EUOXYSTELMA*,



the corona vesicles are attenuate apically, forming long, incurved processes exceeding the stigma-head. Towards the base, there may be manifest a decided constriction above the attachment of the vesicle to the column. The latter forms a sort of platform supporting the vesicle in many species.

Variation in the corona vesicles has been much over-emphasized taxonomically in the past, although the dangers of such a course have been stressed by most authorities on the family. Examination of herbarium material of all the species, supplemented by greenhouse and field observation of a number, has convinced me that, while the corona-shape potentialities are constant in the species recognized here, developmental upsets of one kind or another may modify their actual shape considerably, especially in subg. *OXYSTEMMA* (cf. *S. Gilliesii* and *S. campanulatum*). The presence or absence of an apiculation, or the degree of compression, must not be overly stressed where individuals are concerned.

All these elaborations of the androecium apparently have arisen as a result of natural selection operating in conjunction with entomophily. The method of pollination recently has been described and illustrated for *Asclepias*<sup>36</sup> and a detailed discussion is not necessary here. The essentials of the process are well known, but a clear understanding must await sedulous biological study. It is speciously simple to assign roles to the various components of the complicated flower, but many aspects will have to be re-examined. For example, it is seldom realized that in most cases the corona and other floral appendages serve not so much to attract insects as to guide their legs into the proper position for pollination. In its search for the abundantly secreted nectar (which is well advertised by a heavy fragrance), an insect scarcely can avoid getting its feet or various bristles upon its body caught in the anther-wings at the basal opening. Once caught, there is no escape without withdrawing a pollinium.

According to the terminology which I shall employ, each pollinium consists of two pollinium-sacs which are joined by the translator arms (or caudicles) to the corpusculum. The translator arms and the corpusculum, sometimes called the "gland," make up the translator apparatus. Each pollinium-sac consists of the contents of one locule of the anther, enclosed by a yellowish, elastic substance of a waxy appearance. This investing layer about the pollen apparently is secreted by the tapetum at an early stage in development. The pollinium-sac is essentially oblongoid-cylindrical, but gibbous in outline, and the more strongly curved edge is toward the connective of the anther. At the time that the pollinium-sacs are being formed, the glandular surface of the stigma-head is secreting a substance not unlike that surrounding the pollen. While this process has been described both in English<sup>37</sup> and in German<sup>38</sup>, the details are not known widely. The essentials have been confirmed for *Sarcostemma*. The result of this secretion, deposited at

<sup>36</sup>Woodson, op. cit. 198-199. 1941.

<sup>37</sup>Corry, Thomas H. Structure and development of the gynostegium and the mode of fertilization in *Asclepias cornuti* Decne. (*A. syriaca* L.), Trans. Linn. Soc. II, 2:173-207. 1884.

<sup>38</sup>Demeter, Karl. Vergleichende Asclepiadeenstudien. Flora, n. s. 15:130-176. 1922.



varying rates and times, is the translator apparatus, one of the most remarkable structures in the plant kingdom.

That portion of the stigma-head above the alar chamber is creased by a furrow along the same axis as the anther-wings. The margins of this furrow secrete first and they form two bars of a substance which, initially soft and yellow, hardens and becomes deep brown. Subsequently the entire furrow begins to secrete, and the two bars thus become connected at the back by a thin plate. At the same time, however, the stigma-head is developing and slowly changing in size and shape: by differential growth, the margins of the furrow and their secreted bars are pushed forward and toward one another as the furrow increases in size at the back. The corpusculum at this stage is in the form of a clip, the free ends curving inwards. It is easy to see, then, why the name "gland" is inappropriate for the corpusculum, for it not only secretes nothing itself but is scarcely adhesive as was formerly believed.

Rather late in development, two bands of tissue of the stigma-head, extending from the corpusculum to the pollen-sacs of contiguous anthers, secrete the material which forms the translator arms. Because of their relative thinness, the translator arms clearly show the imprint of the epidermal cells which secreted them; the result is that they appear cellular to superficial observation. The corpusculum, on the other hand, is so thick that it is only in sections or whole mounts cleared in lactic acid that one can discern the slender bars of secrete of which it is constituted. In carefully made sections these may even be referred to the cells from which they were produced.

Several days before the bud opens, the ventral wall of the anther begins to disintegrate across a relatively wide area at the apex of each locule and this continues until each pollinium-sac is exposed at the back. The distal end of the caudicle, being the last portion to be secreted and protected from desiccation, is still soft and adhesive, and it apparently contacts the upper corner of the pollinium-sac and fuses with it. In *Sarcostemma*, there is a perceptible joint between the two separately formed structures. In other genera, however, the translator arm merges gradually with the substance of the pollinium-sac envelope. At the time of anthesis the translator arms are soft and flexible, and because of a difference in thickness of the secreted material and of the curvature of the stigma-head have developed a torsion which causes them to turn at right angles to the plane of the corpusculum, when removed from the flower. By this motion the attached pollinium-sacs are caused to rotate  $90^\circ$  so that the more convex side is turned toward the back. Thus it comes about that the two bags of pollen lie in parallel planes instead of in the same plane as they did in the flower.

The corpusculum usually is broadly sagittate, but may be narrowly so, or ellipsoid. As a consequence of the method of its secretion, it is canaliculate and the canal, in the form of a cone, is open along the front forming a cleft. The latter is aligned with the alar chamber so that if a bristle of the proper size is introduced into the alar chamber at the base and pulled upward, it is drawn into



the corpusculum and wedged firmly in the cleft. When withdrawn from the flower, the bristle then carries with it the pollinium, the two pollinium-sacs rotating slowly as the caudicles dry. Should the same bristle be inserted similarly into another alar chamber, it is the translator arm attached to one pollinium-sac which is caught in the anther-wings, while the other remains outside of the chamber. At the top of the alar chamber the pollinium-sac is abruptly caught against the projecting stigma-head and it breaks from the translator arm. The latter, thus freed, passes into the cleft of the corpusculum of the new pollinium, which is then withdrawn. This process of insertion and removal produces the dichotomous or unilateral combinations of pollinia called multiple pollinia. I have observed multiple pollinia composed of more than twenty pollinia; and, in one instance, a small insect formed a bridge between two pollinia.

Judging from the relatively high frequency with which they occur in the species which I have examined, multiple pollinia are a regular and natural occurrence in many asclepiads. Robertson<sup>39</sup> has discussed the importance of multiple pollinia to species of *Asclepias* with large gynostegia which catch fewer processes on an insect's leg. In such cases, they afford a greater chance of insertion since broken caudicles appear to be more easily caught than insect bristles and since the long multiple structures are guided more efficiently into the anther-wings by the corona segments. By means of multiple pollinia an insect can carry many more pollinia than the available bristle space would allow were each bristle to bear but one corpusculum.

When described, the process of pollination seems hopelessly complex and laborious, yet when the proper instrument of pollination is employed it is surprisingly easy to perform. In *Sarcostemma bilobum* ssp. *Lindenianum*, for example, where the orifice of the alar chamber is sufficiently large to admit a fine dissecting needle, I have produced multiple pollinia with little difficulty; a fine hair is suitable for species with smaller flowers. Brown<sup>40</sup> and Robertson<sup>41</sup> have noted the amazing rapidity with which the proper insect is able to effect pollination. Often the action is quicker than the eye can follow. If one watches the flowers for even a short period he is certain to see many insects, attracted by the sweet fragrance, crawling over the umbels of flowers and probing for nectar among the corona segments. The weight of the insect makes the flower, or entire inflorescence, suddenly top-heavy, and, as it begins to tilt, the insect grasps the only structures which afford support, the projecting anther-wings. Rarely is an entire leg caught by the alar chamber; usually only a bristle or row of setae upon the leg or abdomen slips into the orifice, and with a single swift movement of the insect, a pollinium is withdrawn. Pollination is only slightly more difficult, requiring the insect to give an extra tug which breaks the pollinium-sac from the caudicle.

<sup>39</sup>Robertson, Charles. Insect relations of certain Asclepiads. I. Bot. Gaz. 12:214. 1887.

<sup>40</sup>N. E. Brown, in an appendix to Corry, op. cit. 1884.

<sup>41</sup>Robertson, Charles. Notes on the mode of pollination of *Asclepias*. Bot. Gaz. 11:269. 1886.



I should mention that in *Sarcostemma* the majority of mature flowers taken from herbarium specimens were found to have been pollinated at least once. Usually no more than three pollinia are inserted into the alar chambers of a single flower, but it is by no means uncommon to find a flower completely pollinated. Only very rarely have I seen a single pollinium-sac removed from its locule with the other still in place, and I have never observed a pollinium-sac which had produced pollen tubes while still within the locule.

It would appear that cross-fertilization is the rule in those species of Asclepiadaceae which have been studied. Some, like *Asclepias syriaca*,<sup>42</sup> *A. curassavica*, and *A. nivea*<sup>43</sup> are self-sterile. In others it appears likely that the behavior of the translator arms in turning the pollinium-sacs into the right plane for insertion between the anther-wings, a matter of one or two minutes time, would lead to cross-pollination, even if there were no other mechanism for insuring this.

The family Asclepiadaceae has been divided into two sharply distinct subfamilies on the basis of the structure of the translator apparatus and related floral differences. The pollinia of the Cynanchoideae, described in preceding paragraphs, may be visualized to have evolved from simpler structures in the Periplocoideae and Apocynaceae according to the interesting studies of Demeter.<sup>44</sup> In the genus *Apocynum* (Apocynaceae), the first semblance of a translator apparatus is found. Here the stigma-head secretes five thin, quadrangular plates which alternate with the stamens. These are enclosed within cartilaginous margins of the anthers (similar to the anther-wings) and are adhesive, catching the pollen which is discharged from the anthers in tetrads. This pollen-bearing structure then becomes stuck to the appendages of insects which visit the flowers and thus disperse the pollen.

The Periplocoideae also discharge the pollen in tetrads. The latter fall from the anthers into rather complicated translators which are divided into three parts: an upper spoon- or cone-shaped structure which is adhesive and contains the tetrads, a lower adhesive disc which becomes attached to the insect, and a central connecting stalk. After studying the method of formation of the translator and certain teratological forms, Demeter<sup>45</sup> concludes that the spoon or cone is homologous to the corpusculum and that the adhesive disc is comparable to laterally conjoined translator arms. Changes in the shape of the stigma-head and in the distribution of the secretory cells can be imagined which would lead to the formation of a typical pollinium.

Although the occurrence of pollen grains grouped into tetrads is scattered throughout the flowering plants, the formation of pollinia has been reported only for the Asclepiadaceae, the subfamily Mimosoideae of the Leguminosae, and the

<sup>42</sup>cf. Stevens, O. A. Cultivation of milkweed. N. Dak. Exp. Sta. Bull. 333. 19 pp. 1945; and Sparrow, K. K. Types of pods of *Asclepias syriaca* found in Michigan. Jour. Agr. Res. 73:65-80. 1946.

<sup>43</sup>I have been unable to self-pollinate or to hybridize *A. nivea* or *A. curassavica* in the greenhouse, despite repeated attempts.

<sup>44</sup>Demeter, op. cit. 174. 1922.

<sup>45</sup>Demeter, loc. cit.



Orchidaceae. In the Chlaenaceae, a small family of the Malvales, there are multiple groups of four or sixteen pollen grains enclosed within a deeply furrowed wall.<sup>46</sup> This wall has been interpreted as the modified spore-mother cell wall, and, if this interpretation is correct, these aggregates cannot be referred to as pollinia (as their describer recognizes). The pollinia of the other three groups are characterized by having the pollen grains merely adherent, with or without a thick matrix, and not enclosed within a single cell wall.

In the Mimosoideae, the pollen is in tetrads or aggregated into pollinia of relatively few grains, in an ovoid mass which bears at the pointed end an adhesive substance apparently derived from the tapetum. The stigma is a simple, obscurely sulcate, capitate structure, and there are no special devices for receiving the pollinia.

The Orchidaceae show an interesting series from pollen in tetrads to various types of pollinia. In the more primitive forms each locule produces many small pollinia similar to those of the Mimosoideae, but these are held together into packets by viscid threads derived from the tapetum. These compound pollinia may be attached by slender, elastic caudicles to an adhesive disc which is the secretion of the rostellum, a sterile portion of the stigma. In certain species, the sticky substance secreted by the stigma is first applied to the head of a visiting insect, and the pollinia subsequently fall from the anthers into this substance and become affixed. Pollinia of the more advanced type are compact, waxy structures borne upon rather specialized caudicles which are attached to an adhesive, cellular disc. In this case, a layer of tissue of the rostellum has abscised, carrying with it the sticky secretion. The caudicles undergo various movements which put the pollinium into the proper position for pollination.

In general, the pollinia of the orchids are much less specialized than those of the Asclepiadaceae. The rostellum is, in a sense, comparable to the secretory stigma-head, and the caudicles and adhesive disc have been compared with the translator arms and corpusculum of the asclepiads. These similarities are rather superficial, however. Furthermore, the structure of the stigmatic chamber in the orchids is by no means as directly related to that of the pollinia as it is in the milkweeds, a fact which perhaps accounts for the more frequent occurrence of natural hybrids in the orchids in contrast to the asclepiads. On the other hand, in the transformation of the perianth into the most outlandish structures, and in the development of special insect food tissues or of pseudocopulation, the orchids have far surpassed the Asclepiadaceae.

The Asclepiadaceae are often mentioned as illustrating mechanical isolation of species and extreme adaptation for insect pollination, but few persons have realized the delicacy and precision of the relationship. While pollination can easily be accomplished by the right pollinator, it must be emphasized that there are so many elements involved in the process that, if any one is incompatible with any other,

<sup>46</sup>Smith, C. C. A case of "pollinia." *Phytologia*. 1:83-88. 1934.



it fails. That most assiduous, but apparently almost forgotten work of Charles Robertson<sup>47</sup> has made this quite clear. Precisely to what part of an insect's body a pollinium will be attached is determined by the structure and height of the corona, the length of the column, the structure of the anther-wings, the structure of the stigma-head, the shape of the corpusculum, etc. Robertson<sup>48</sup>, for example, found that bumble-bees may have pollinia of *Asclepias Sullivantii* on their claws, of *A. verticillata* on their tarsal hairs, and of *A. longifolia* on the hairs of the ventral surface. These three species, although in bloom at the same time and employing the same efficient pollinator, are nevertheless practically incapable of hybridization. While visiting a flower of *A. Sullivantii*, the bumble-bee deposits only pollinia of that species, because only they are in a position to be inserted and caught in the alar chamber. If it should happen that pollinia of *A. verticillata*, upon the tarsal hairs, were caught between the gaping anther-wings of *A. Sullivantii*, they are so small that they would be withdrawn without affecting the plant in any way. Conversely, the pollinia of *A. Sullivantii*, the flowers of which are about three times the size of those of *A. verticillata*, cannot be inserted into the alar chamber of the latter under the dissecting microscope, much less by the bumbling bee. Similar relationships are found between *A. longifolia* and the other two species; in size, the flowers approach those of *A. verticillata*, but the anther-wings and pollinia have a completely different structure.

Further evidence for the rigidity of the interrelation of flower and insect is provided by the multiple pollinia. I have never found these combinations to include more than one kind of pollinium (and the morphology of a pollinium often is sufficient to define a species in *Sarcostemma*). There is, thus, what might be called a lock-and-key relation between the pollinia and the alar chamber. It is only the proper key, the pollinium-sac, which can be inserted into a given lock, the alar chamber, so that fertilization will take place. Moreover, the key must be in the proper hands to gain access to the lock.

We may inquire into the effects of the intimate relationships between the milk-weeds and their insect-pollinators, and although we cannot yet answer the question, we can perceive that the effects are far-reaching ecologically, genetically, morphologically, and taxonomically. The plant is dependent upon a particular type of pollinator, and both the plant and the insects in its environment must have evolved more or less together. *Sarcostemma pannosum*, from western Mexico, when grown in St. Louis was visited by many insects, but no pollinia were withdrawn and no fruit produced. A plant, on the other hand, may have a profound effect upon the insects, aside from that of supplying them with food. It is well known that insects sometimes are caught by the corpuscula which they are not sufficiently strong to remove, and they perish on the flower. Indigenous forms

<sup>47</sup>Robertson, Charles. Notes on the mode of pollination of *Asclepias*. Bot. Gaz. 11:262-269. 1886. Insect relations of certain asclepiads. I & II. *ibid.* 12:207-216, 244-250. 1887; Flowers and insects, Asclepiadaceae to Scrophulariaceae. Acad. Sci. St. Louis. Trans. 5:569-577. 1891.

<sup>48</sup>Robertson, *op. cit.* p. 250. 1887.



must be caught rather rarely when one considers that the number of visitors to a single flower runs into very high figures. However, for the hive-bee, introduced into our fauna, the situation is different. In a period of seventeen days, Robertson<sup>49</sup> found 671 dead bees in the flowers of a patch of *Asclepias Sullivantii*. Furthermore, this species, which fastens its pollinia to the claws of insects, may so fetter a bee with pollinia that it is expelled from the hive as a result of its inability to collect honey and to climb upon the combs. Of course, *A. Sullivantii* is not benefited, for, as Robertson puts it: ". . . it seems that the flowers are better adapted to kill hive-bees than to produce fruit through their aid."

Genetically, a situation results in which the species are isolated mechanically from hybridization with one another, yet usually are cross-pollinated with other individuals of their own species. Two species, then, as isolated as if one had migrated into a different habitat, may respond with striking specializations in floral structure but undergo little or no change in vegetative organs. One need only compare species of *Gonolobus*, *Marsdenia*, and *Cynanchum* from Mexico or South America to see that often only slight differences, in the structure and arrangement of the trichomes, for example, distinguish them vegetatively. Yet the floral differences are so great that they are used to characterize categories of tribal rank.

This field of inquiry is one which still scarcely has been touched. It will require much patient field work before a picture of the dynamics of any one species can be worked out. A taxonomic monograph can serve to indicate some of the problems, however, and should function as a framework, albeit flexible, within which they are interpreted. It is of considerable interest to note that in several closely related species of *Sarcostemma* which occupy the same or contiguous areas, there are differences in the shape of the pollinium-sac and corpusculum and complementary differences in the anther-wings which would make hybridization very difficult. If one examines the key to the species of the series CYNANCHOIDES, he will notice how many groups of species are segregated by differences in the structure of the pollinium, the length of the column, or the degree of apiculation of the stigma-head. This, in all probability, explains the rarity of hybridization and those evolutionary processes associated with introgression which are proving to be of such importance in other families of plants and animals. Certainly the Asclepiadaceae offer fascinating subjects for the evolutionary biologist.

The conjoined stamens and gynoecium make up a structure called the gynostegium, the name referring to the fact that the androecium completely roofs over the carpels. The stigma-head exposed at the top is more complicated than might appear at first sight. The apex is papillate and may be obscurely bilobed or bear two long apiculae. The degree of apiculation, however, is somewhat variable, and characters of the stigma-head must be used with discretion. The rather massive body of the stigma-head contains two central strands of short, spirally thickened cells. These are a continuation of the vascular strands of the styles which gradually

<sup>49</sup>Robertson, op. cit. p. 211. 1887.



attenuate toward the apex only to enlarge within the stigma-head to form a core of considerable dimensions. Their function appears to be to support and to strengthen, since in other genera they extend nearly to the surface and, flaring broadly, form a subepidermal layer of sclereids.

The papillate apical portion of the stigma-head is distinct from a lower, non-papillate region which projects, shelf-like, laterally. On the upper surface of this area are the five furrows in which the corpuscula are secreted. Lateral to these are the less prominent grooves in which the translator arms are produced. Below this region the stigma-head is abruptly constricted to the styles. Upon this lower surface is the receptive surface of the stigma and below this, the attachment of the flange of the staminal tube.

Corry<sup>50</sup> has stated that the receptive area of the stigma-head is a continuous ring, similar to that in the Apocynaceae, above the attachment of the staminal tube. Whether or not this is so can be determined only by laborious experimentation; the fact remains that the stigma-head is functionally receptive only at the five points which are accessible to the alar chamber, i. e. alternating with the stamens. In order for pollination to be effected, a pollinium-sac must be drawn between the anther-wings at the base and up against the stigma-head where it breaks from the caudicle. In many species there are projecting ridges within the alar chamber which firmly grip the pollinium-sac and hold it in the proper position. In this moist chamber, the pollen tubes grow, in the form of a skein, into the stigma and down the styles to the ovary. Although apparently all of the pollen grains germinate, the pollen tubes are found to escape only from a rather small area along the more convex edge of the pollinium-sac, which is always the edge towards the stigma in the alar chamber. This occurs whether they are germinated in the flower or in a sugar solution.

The two carpels are free nearly to the base and are somewhat sunken in the receptacle. Alternating with them are two small papillae, the nature of which is completely unknown. Devoid of vascular tissue, they may be the result merely of compression of the receptacular tissue by the confining corolla tube, or the vestiges of carpellodes. Very rarely one finds that three carpels have been produced, but conditions within the lower corolla tube are so crowded that it is difficult to determine if the small papillae still are present. The anatropous ovules are borne upon axile placentas and the micropyles are directed outwards.

Ordinarily only one carpel of a pair develops into fruit, although two is the rule in several species. The paucity of fruit, as compared with flowers, has been attributed to difficulty in pollination. This clearly is not the case in the forms which I have studied, for not only is pollination a simple matter for the right insect, but it is not uncommon to find inflorescences in which a majority of flowers have young fruit. Yet, in these same species, only a single follicle, or several, is to be found in a mature condition in an inflorescence. The matter appears to

<sup>50</sup> Corry, op. cit. p. 175. 1884.



relate to nutrition rather than fertilization. Moore<sup>51</sup> attributes the collapse of pods in *Asclepias syriaca*, in part at least, to competition for food between the endosperm and the adjacent maternal tissue in the ovules.

The follicles in *Sarcostemma* are narrowly fusiform to obclavate, except for *S. pannosum* and the Argentine race of *S. clausum*, where they are inflated at the base. According to Teodoro Meyer<sup>52</sup>, the corky, inflated follicles of this race of *S. clausum* are adapted for floating.

The seeds are unequally biconvex or complanate. Usually the dorsal side is more or less rugose, and the flatter, ventral side bearing the obscure raphe, minutely papillate. The margin is flattened and may be serrate at the chalazal end. The white or yellowish coma is produced at the micropylar end of the seed. In the Asclepiadaceae, the coma arises from the rim of the micropyle on the side toward the funicle and does not encircle the micropyle.<sup>53</sup> The presumptive papillae scarcely are apparent in the flower at anthesis, but after fertilization they undergo remarkably rapid growth to produce the apparatus for wind transport so characteristic of the family.

There are few reliable taxonomic characters in the fruit and seeds. It is only with considerable experience with a genus that one can safely identify fruiting specimens in the Asclepiadaceae.

#### GEOGRAPHY

While particular geographic problems will be discussed under the species to which they pertain, it may be of interest to present a general picture of the distribution of *Sarcostemma*.

The subgenus *CERAMANTHUS* includes species from southwestern United States to northern Argentina. The center of diversity is in Mexico, from whence the species extend into more or less xeric habitats, at low to moderate altitudes, to the north and south. In northern Mexico and in the southwestern United States, the plants inhabit dry, sandy washes or arroyos, and they show morphological reduction in a number of aspects. The few specimens which have been collected from less restrictive habitats, such as drainage ditches, have much larger flowers and leaves. In southern Mexico and in South America, the plants attain greater size, although they still prefer such drier areas as savannas or forest margins. On the llanos of Argentina, the halophytic *S. gracile* again shows reduction.

*Sarcostemma clausum* has the widest range of the species in this subgenus, extending from Sonora and Florida to northern Argentina. It has developed numerous local variants of pubescence, leaf shape, and peduncle length, which have not been recognized taxonomically. It is unfortunate that the paucity of specimens from South America does not permit a detailed analysis of this interesting species.

<sup>51</sup> Moore, Raymond J. Investigations on rubber-bearing plants. III. Development of normal and aborting seeds in *Asclepias syriaca* L. Can. Jour. Res. 24C:64. 1946.

<sup>52</sup> Meyer, T. Los generos "Funastrum" y "Philibertia." Lilloa 9:430. 1943.

<sup>53</sup> Hildebrand, F. Über die Entwicklung der haarigen Anhänge an Pflanzensamen. Bot. Zeit. 30:233, 257. 1872.



The species of the subgenus *OXYSTELMA* are divided among three sections, one of which is limited to the Old World. In the New World, the species of § *PHILIBERTIA* and § *PENTACYPHUS* occur in Andean South America, being centered, with respect to diversity, in northern Argentina and adjacent Bolivia. Like the species of subg. *CERAMANTHUS* in preferring more or less arid habitats, the American oxystelmas occur at moderate to high altitudes.

The single Old World species of subg. *OXYSTELMA* is *Sarcostemma* (§ *EUOXYSTELMA*) *esculentum*, which is a weedy plant ranging from Egypt through India to the islands of the East Indies. Apparently it grows in forest clearings and margins, especially along water courses. Its distribution possibly has been affected by man, for it occasionally is cultivated for its fruit and often is found in flower gardens because of its striking flowers.

The leafless sarcostemmas of subg. *EUSARCOSTEMMA* range from southernmost Africa and Madagascar, up the eastern coast of Africa to India, the East Indies, and Australia. They are plants of very dry, rocky or sandy areas, and their adaptation to these xeric habitats is manifest in the scale-like leaves and succulent, photosynthetic stems.

There are thus four main groupings of the species of *Sarcostemma*, which coincide in part with and substantiate the natural subgeneric groups recognized here. They suggest, also, that the genus itself is, in a sense, unnatural in that it includes several distinct evolutionary entities. This idea will be discussed further in the section on relationships. These major geographic and systematic groups include, then, the predominantly Mexican and Central American subg. *CERAMANTHUS*, the Andean subg. *OXYSTELMA*, § *PHILIBERTIA* and § *PENTACYPHUS*, and the two superposed Afro-Asian subg. *OXYSTELMA*, § *EUOXYSTELMA* and subg. *EUSARCOSTEMMA* (which do not appear to be closely related).

Although the systematics of the Old World forms is confused thoroughly at the specific level, it is possible to make certain comparisons between the subgenera and sections with respect to the number of species and degree of specialization and endemism which is apparent in each.

The subgenus *CERAMANTHUS* is the largest group, comprising fourteen closely related species which have been arranged taxonomically only in morphological series. Of these species, one is widespread, ten are of moderate extension, and three are rather strict endemics. Nearly all but the endemic species show one or several infraspecific groups at various levels of differentiation.

In the subgenus *OXYSTELMA*, there are nine species which break apart sharply into sections. In the Western Hemisphere, § *PHILIBERTIA* comprises five species which are fairly localized in their distribution; one species, however, is endemic to a small area in Argentina; another extends from southern Bolivia to south-central Argentina. About half of these species have developed infraspecific variants. The two species of § *PENTACYPHUS* are very distinct morphologically; again, one is rare, the other of moderate range.



*Sarcostemma* (§ EUOXYSTELMA) *esculentum* appears to be rather homogeneous throughout its range, differing only in vegetative characters and details of the fruit, and showing no tendency toward the striking floral variation of the New World forms. In this sense, it is comparable to *S.* (CERAMANTHUS) *clausum*, although it is the only species in the section and is very complex florally.

While it cannot be stated exactly to what degree the species of subg. EUSARCOSTEMMA are localized, it would appear that most have relatively wide distributions. Yet these species again seem to be very much alike in floral structure across their distribution from Africa to Asia.

These differences in degree of homogeneity and restriction to particular areas are rather interesting. They suggest that, of the three subgenera, CERAMANTHUS is undergoing the most rapid evolution at present. Subgenus OXYSTELMA appears to have achieved greater stability in certain respects, but in the New World is still becoming more diversified. On the other hand, the rather meagre evidence from the Old World seems to indicate that the species there are not actively developing new forms or are specializing along different lines.

#### RELATIONSHIPS

It has been mentioned that the taxonomy of the Asclepiadaceae is in a very confused state. Until a general system has been developed for the family, discussions of relationships and phylogeny scarcely will be intelligible. At present, the family is split into the Cynanchoideae, comprising the typical Asclepiadaceae with pollinia, and the much smaller, exclusively Old World, Periplocoideae, in which true pollinia are lacking. These divisions are discontinuous and undoubtedly natural, but the smaller subdivisions are less satisfactory.

The Cynanchoideae have been divided into four tribes: Asclepiadeae, Secamoneae, Tylophoreae, and Gonolobeae.<sup>54</sup> The Secamoneae, which have 4-locular anthers and occur only in the Old World, need not concern us. Woodson<sup>55</sup>, after critical study of the other three tribes in North America, has presented a key to the tribes, the novel feature of which is his use of the sculptured, partially sterile pollinia of the Gonolobeae as a major character. The Asclepiadeae and Tylophoreae are distinguished, as is customary, by the position of the pollinia, i. e. whether pendulous or erect, respectively. Although the Gonolobeae have been defined unmistakably, the distinction between the two tribes with uniformly fertile (with but rare exceptions), unsculptured pollinia seems not yet sufficiently decisive.

*Sarcostemma* is referred to the tribe Asclepiadeae of the Cynanchoideae. Since the genera which have been placed in synonymy have been drawn from three of Schumann's subtribes, no attempt will be made to allocate the genus to one of his artificial subdivisions. For the present, it must suffice to point out the morphological relationships of the genus.

<sup>54</sup>Schumann, op. cit. 1897.

<sup>55</sup>Woodson, op. cit. 1941.



*Sarcostemma* is closest to *Cynanchum* and *Blepharodon*. The coronal appendages of *Cynanchum* usually are laminate and variously lobed or united. There are species, however, in which the corona lobes in life are quite fleshy so that little modification need be imagined to produce an inflated structure comparable to that of *Sarcostemma*. In those forms, however, the anther wings usually are not turned at an angle to the plane of the anther, nor are the pollen sacs usually apparent on the back of the anthers, as is characteristic of *Sarcostemma*.

The genus *Blepharodon* consists of two groups of species. Those typified by *B. nitidus* have corona segments which may be considered to consist of two radially arranged, laminate lobes partially fused by their margins. The second group, of which *B. mucronatum* is an example, has semi-vesicular corona segments which are open apically or closed by a thin membrane. In detail they are similar to those of the first group. Thus, from the standpoint of the corona, *Blepharodon* might be considered more or less transitional between *Cynanchum* and *Sarcostemma*. From the latter it differs in the saccate or vesicular corona segments, the anther wings usually in the same plane as the anther, and the very short caudicles bearing pyramidal pollinium-sacs. These same characters, however, together with details of the androecium and stigma-head, preclude relating the genera in linear sequence. Neither *Cynanchum* nor *Blepharodon* has a corona ring, though occasionally there are structures in each which might be mistaken for such.

I am not yet able to discuss satisfactorily the evolutionary relationships of the species of *Sarcostemma*, except for the statements made in connection with the section on geographical distribution and the discussion of certain minor trends which will be noted under the individual species. The plants apparently all have evolved toward the xerophytic type, for the most complex florally are the most specialized in this respect. In most cases the species have developed mechanical isolating mechanisms based on floral structure. Reasoning by analogy with the Asclepiadaceae which have been studied cytologically, it does not seem likely that polyploidy has played a significant role in the evolution of the genus.

I believe that the three subgenera and several sections recognized here are reasonably natural groups encompassing closely related species. Their aggregation into a broadly inclusive and arbitrary genus perhaps needs some explanation. While it may be our ideal to have a taxonomic system which expresses precisely the phylogeny of the organisms involved, the facts of evolution all too often do not permit this. Thus while species in the Asclepiadaceae generally are very well-marked, genera are extremely difficult to delimit. When the entire range of variation is considered, certain centers of variation can be perceived, and it would seem that these should be the basis for building up of genera by accretion, as it were. This has not been done, however, and the description of many small, ill-correlated genera has created a chaotic situation. Because of the nature of taxonomy and nomenclature, the only remedy is the establishment of inclusive, even if somewhat arbitrary, genera which will integrate these smaller groups into a usable system.



## MATERIALS

Specimens from the herbaria of the following institutions have been studied:

Chicago Museum of Natural History.  
 Dudley Herbarium of Stanford University.  
 Gray Herbarium of Harvard University.  
 University of Cambridge.  
 Missouri Botanical Garden.  
 Museum National de l'Histoire Naturelle, Paris.  
 Naturhistoriska Riksmuseet, Stockholm.  
 New York Botanical Garden.  
 Royal Botanic Gardens, Kew.  
 United States National Herbarium.  
 University of California, Berkeley.

I am indebted to the curators of these herbaria for the loan of this material, including many valuable types. I also wish to thank the staff of the Missouri Botanical Garden and its director, Dr. G. T. Moore, for the use of the library and herbarium facilities. To Dr. R. E. Woodson, Jr., I am especially grateful for his generous advice and invaluable constructive criticism.

For species in the United States, only one specimen per county has been cited. For those in other countries, nearly complete citations have been given. Data on habitat and blooming and fruiting time are summarized in the discussion following the description. The distribution maps include all specimens examined which could be located precisely. However, a complete list of all the plants examined is provided in the Index to Exsiccatae, together with the number of the species to which they are referred in this account.

## TAXONOMY

SARCOSTEMMA R. Brown, in Mem. Wern. Soc. 1:50. 1809, emend. R. Holm.

*Oxystelma* R. Br. loc. cit. 40. 1809.

*Philibertia* HBK. Nov. Gen. et Sp. Pl. 3:195. 1819.

*Pentagonium* Schauer, in Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1:364. 1843.

*Lugonia* Wedd. Chlor. And. 2:49. 1857.

*Zosima* Phil. Sert. Mend. Alt. 29. 1871, non Hoffm.

*Funastrum* Fourn. in Ann. Sci. Nat. Bot. VI, 14:388. 1882.

*Cystostemma* Fourn. in Mart. Fl. Bras. 6<sup>4</sup>:204. 1885.

*Philibertella* Vail, in Bull. Torr. Bot. Club 24:305. 1897.

*Ceramanthus* (Kunze) Malme, in Ark. Bot. 4<sup>14</sup>:2. 1905, nec Hassk. nec Hook. f. (based on *Sarcostemma* subg. CERAMANTHUS Kunze in Linnaea 20:26. 1847.)

*Pentacyphus* Schltr. in Engl. Bot. Jahrb. 37:605. 1906.

*Tetraphysa* Schltr. loc. cit. 616. 1906.

Suffrutescent, dextrorsely twining or trailing vines, rarely semi-erect, the stem variously little- or much-branched. Leaves usually laminate, sometimes reduced to scales, usually with one or more glands on the ventral surface of the midrib at the base; stipules minute. Inflorescences extra-axillary, cymose, racemiform to umbelliform, 1- to 30-flowered; peduncle present or absent. Calyx 5-lobed nearly to



the base which is adnate to the corolla, usually with 1 to many alternate or indefinitely distributed squamellae within. Corolla 5-lobed, rotate-subcampanulate, campanulate, or salverform. Stamens 5, the filaments coherent to form a column (rarely obsolete), usually produced at their insertion upon the corolla to form a patelliform corona ring often completely adnate to the corolla or to the filaments directly below the anthers, each filament bearing an inflated, vesicular segment (corona vesicle) directly below the anther; anthers 2-celled, the thecae apparent dorsally, the alae usually at  $45^\circ$  to the anther, the membranous dorsal appendage ovate to deltoid; pollinium-sacs oblongoid-cylindrical to clavate, nearly uniformly rounded or flattened, uniformly fertile (rarely with a small sterile region at the attachment of the caudicle), the corpusculum sagittate to ellipsoid, the slender caudicles exceeding the corpusculum in length, rarely very short. Carpels 2, somewhat subinferior, free towards the base, prolonged above into relatively conspicuous styles which unite to form a convex to 2-apiculate stigma-head. Follicle fusiform to obclavate; seeds unequally biconvex or flattened, with a micropylar coma.

Type species: *Sarcostemma viminale* (L.) R. Br.

#### KEY TO THE SUBGENERA

- A. Stems never succulent; leaves laminate; inflorescence racemiform to umbelliform, the peduncle usually manifest; corolla rotate-subcampanulate, campanulate, or salverform; vesicles of the corona ovoid or obovoid to oblongoid or spheroid, ring of the corona free or adnate to the column directly below the anthers.
  - B. Corolla rotate-subcampanulate or salverform; ring of the corona free from the corolla, porrect (lacking in *S. flavum*); inflorescence corymbiform to umbelliform, 4- to 30-flowered. Species of the Western Hemisphere ..... Subgenus I. CERAMANTHUS (p. 506)
  - BB. Corolla campanulate; ring of the corona adnate to the corolla or more or less obsolete; inflorescence racemiform or umbelliform, 1- to 10-flowered. Species of the Eastern and Western Hemispheres. .... Subgenus II. OXYSTELMA (p. 537)
  - AA. Stems succulent, or woody below; leaves scale-like throughout; inflorescence subumbelliform, the peduncle obsolete; corolla rotate-subcampanulate; vesicles of the corona ovoid, ring of the corona adnate to the filaments. Species of the Eastern Hemisphere..... Subgenus III. EUSARCOSTEMMA (p. 482)

Subgenus I. CERAMANTHUS Kunze, in *Linnaea* 20:26. 1847.

- Philibertia* acc. to Benth. in Benth. & Hook. Gen. Pl. 2:733. 1876, non HBK.
- Funastrum* Fourn. in Ann. Sci. Nat. Bot. VI, 14:388. 1882.
- Cystostemma* Fourn. in Mart. Fl. Bras. 6<sup>4</sup>:204. 1885.
- Philibertella* Vail, in Bull. Torr. Bot. Club 24:305. 1897.
- Ceramanthus* (Kunze) Malme, in Ark. Bot. 4<sup>14</sup>:2. 1905, nec Hassk. nec Hook. f.

Leaves laminate, rarely caducous or reduced; inflorescence corymbiform to umbelliform; corolla rotate-subcampanulate or salverform; ring of the corona usually pronounced (lacking in *S. flavum*).

Type species: *Sarcostemma elegans* Decne.

A closely knit group of species inhabiting drier regions of tropical and temperate America. The keys have been written so that flowers need not be studied critically for identification. Examination of the dried flowers with a hand lens often will provide a reassuring check on vegetative characters, however. All the



species recognized here differ from one another in many aspects of floral structure, but these differences often are difficult to describe adequately. Recourse may be had to the drawings of the gynostegia which have been made to show a condition typical for each species.

## KEY TO THE SERIES

- A. Ring of the corona present. Plants of North and South America.
- B. Inflorescence lateral to the main axis or lateral branch.
- C. Inflorescence corymbiform, obviously compound, the peduncle not equalling the subjacent internode in thickness; leaves usually densely white-tomentose beneath. Plants of Mexico.....Series 1. PANNOSA (Sp. 1)
- CC. Inflorescence umbelliform, the pedicels all inserted at nearly the same point; leaves never densely white-tomentose beneath.
- D. Peduncle equalling or exceeding the subjacent internode in thickness or lacking (when lacking, leaves obtuse to cuneate at the base), frequently bearing two catenulate cymes.....Series 2. CLAUSA (Spp. 2-3)
- DD. Peduncle not equalling the subjacent internode in thickness, or lacking (when lacking, leaves cordate), usually bearing but one cyme. ....Series 3. CYNANCHOIDES (Spp. 4-12)
- BB. Inflorescence terminal to the main axis or lateral branch, the peduncle not equalling the subjacent internode in thickness, or lacking. Plants of the Galapagos Islands.....Series 4. ANGUSTISSIMA (Sp. 13)
- AA. Ring of the corona lacking. Plants of Argentina, Brazil and Uruguay. ....Series 5. FLAVA (Sp. 14)

## Series 1. PANNOSA R. Holm, ser. nov.

Inflorescentia ut videtur lateralis corymbiformis certe composita, pedunculo quam internodio subjacenti angustiore.

Type species: *Sarcostemma pannosum* Decne.

A monotypic series which contains the presumably primitive species of the subgenus. The obviously compound inflorescence characterizes the series.

## 1. SARCOSTEMMA PANNOSUM Decne. in DC. Prodr. 8:540. 1844.

*Sarcostemma rotundifolium* Decne. loc. cit. 1844, ex char. (T.: *Mairet de la Chaux de Fond in Herb. DC.*).

*Philibertia pannosa* (Decne.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:320. 1881.

*Philibertia rotundifolia* (Decne.) Hemsl. loc. cit. 1881.

*Philibertia Pavoni* Hemsl. loc. cit. 319. 1881. (T.: *Ghiesbreght 200 in Herb. Kew.*!).

*Philibertia tomentella* T. S. Brandeg. in Univ. Calif. Publ. Bot. 4:90. 1900. (T.: *Brandeggee 361 in Herb. Univ. Calif.*!).

*Funastrum pannosum* (Decne.) Schltr. in Fedde's Repert. 13:286. 1915.

*Funastrum rotundifolium* (Decne.) Schltr. loc. cit. 287. 1915.

*Funastrum Pavoni* (Hemsl.) Schltr. loc. cit. 286. 1915.

*Funastrum tomentellum* (Brandeg.) Schltr. loc. cit. 287. 1915.

*Sarcostemma tomentellum* (Brandeg.) Woods. in Ann. Mo. Bot. Gard. 28:217. 1941.

Stems twining, minutely pilosulose; lateral branches normally several. Leaves oblanceolate to obovate-elliptic, acuminate to mucronate, broadly and more or less obscurely cordate, 3.5-9.0 cm. long, 1.5-5.0 cm. wide, subcoriaceous, pilosulose above, densely white-tomentose beneath, with one or more glands on the midrib at the base; petiole 1-3 cm. long. Inflorescences corymbiform, 9- to 30-flowered; peduncle 3-7 cm. long, not equalling the subjacent internode in thickness, minutely pilosulose; bracts linear, minute; pedicels 2.0-3.5 cm. long, minutely pilosulose.



Calyx lobes narrowly ovate, 2.5–4.0 mm. long, pilosulose on both surfaces; squamellae absent or solitary. Corolla rotate-subcampanulate, white or cream-colored, the tube 1.5 mm. long, the lobes ovate, acuminate, 7–10 mm. long, pilosulose without, more or less puberulous-papillate within. Gynostegium 4 mm. high, the column 1.5 mm. long. Anthers 2 mm. long, the apical appendage ovate-suborbicular, the pollinium-sacs oblongoid-cylindrical, 1.2 mm. long with sagittate corpusculum; ring of the corona thin, revolute; vesicles of the corona obovoid, 2.5 mm. long. Ovaries 2.5 mm. long, the styles sericeous; stigma-head conical, 2-apiculate. Follicles broadly fusiform-obclavate, 5–7 cm. long, 2.0–2.5 cm. thick, puberulent; seeds unequally biconvex, 2.5–3.0 mm. long, 1.5–2.0 mm. wide, rufescent, rugose dorsally, papillate ventrally; coma about 2 cm. long.

An attractive species, well-marked by the white tomentum on the under-side of the leaf. In the very rare instances when this pubescence is not dense, the inflated follicle and compounding of the inflorescence are diagnostic. At least one segregate species has been based on a lack of undulation of the leaves (*P. Pavoni*). However, I have found that on a single plant of *S. pannosum* in cultivation, the leaves may be plane or undulate. A similar situation obtains in *S. crispum*.

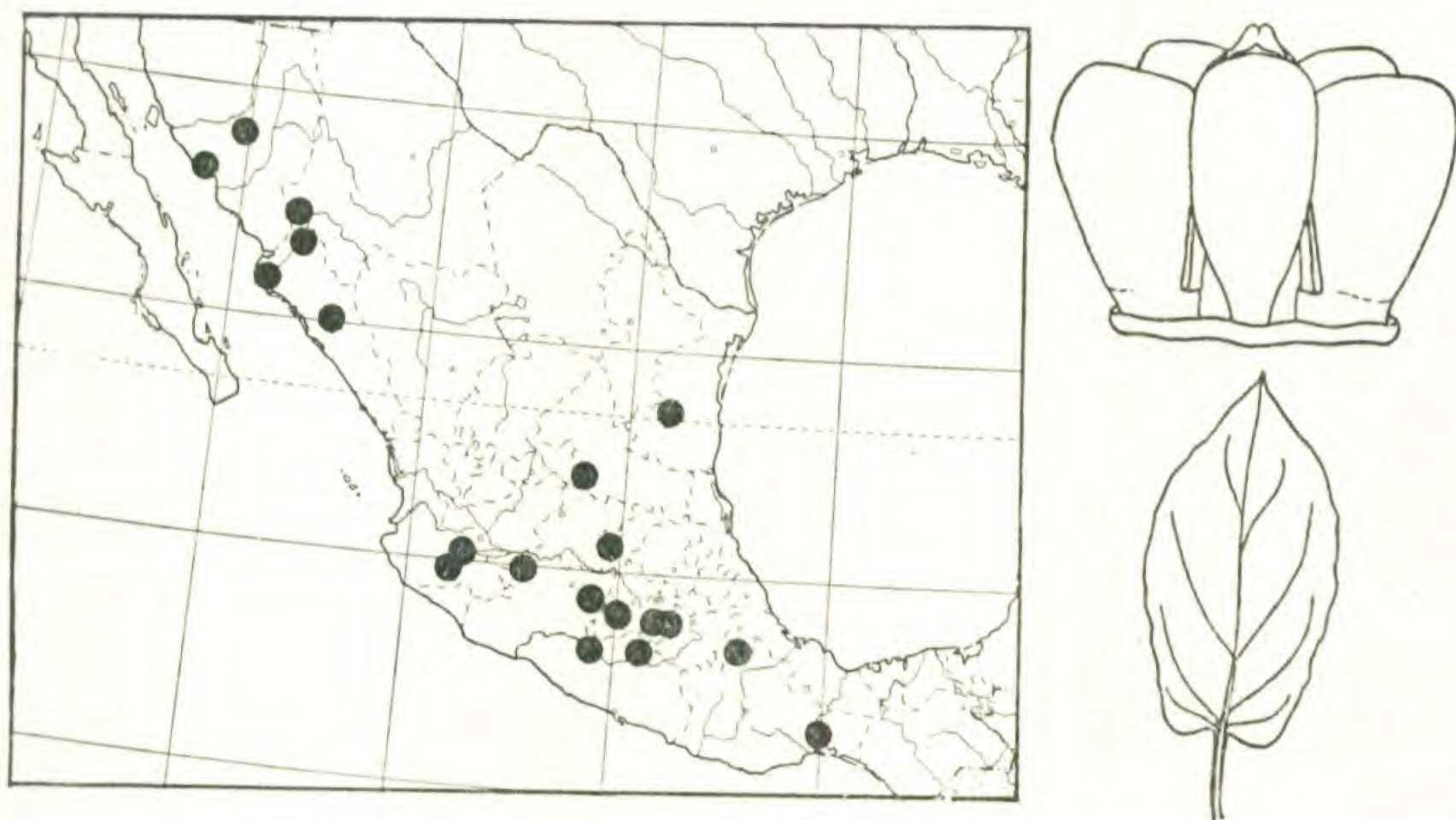


Fig. 5. Distribution, gynostegium, and leaf of *S. pannosum*.

*Sarcostemma pannosum* is endemic to Mexico, where it grows on grassy or rocky slopes from 500 to 6000 feet. It has been collected in flower from July 17 to November 19; fruit has been found from September 22 to November 13.

MEXICO. CHIHUAHUA: Guasarámos, Río Mayo, *Gentry* 2369. DURANGO: loc. unknown, *Rose* 2310. GUERRERO: Pungarabato, Cayuca, *Hinton* 6470; Sierra Madre del Sur, Adama, Temisco, *Mexia* 8861; Placeres, Mina, *Hinton* 10528; Puerta de Oro, Mina, *Hinton* 9175; mts. near Iguala, *Pringle* 13593. JALISCO: Tuxcacuesco, *E. Anderson* s. n.; Río Blanco, *E. Palmer* 340; Sacoaco, M. *E. Jones* 319. MEXICO: Temascáltepec, Vigas, *Hinton* 1191. MICHOACÁN: Monteleón, *Pringle* 11028; near Zamora, *Schery* 182; Tuzantla, Tiquicheo, Zitácuaro, *Hinton* 13077. MORELOS: near Yuatepec, *Rose*, *Painter* & *Rose* 8585; Cuernavaca, *Kenoyer* C220, M. *Martínez* 150/02. NAYARIT: Tepic, Los Bules,



*Goldsmith* 170. OAXACA: San Gerónimo, *Purpus* 7180; Oacalco, *Nagel* 8086. PUEBLA: Coxcatlán, *Purpus* 4118. QUERÉTARO: loc. unknown, *Agniel* 14; near Querétaro, *Rose* & *Rose* 11152; Querétaro, *Kuntze* 23448. SAN LUIS POTOSÍ: Las Canoas, *Pringle* 3227. SINALOA: Culiacán, *E. Palmer* 1492; El Brasil, Rancho Tasajera, Choix, *Montes* & *Salazar* 881; Topolobambo, *E. Palmer* 185; near Labradas, *Ferris* & *Mexia* 5247. SONORA: 9 miles NE of Colorado, between Colorado & Mazatlán, *Wiggins* & *Rollins* 328; Guaymas, *E. Palmer* 195. TAMAULIPAS: near Victoria, *Palmer* 497.

Series 2. CLAUSA R. Holm, ser. nov.

Inflorescentia ut videtur lateralis umbelliformis saepe cymis catenulatis duobus, pedunculo internodium subjacens crassitudine aequante vel excedente (interdum obsoleto).

Type species: *Sarcostemma clausum* (Jacq.) R. & S.

This series includes two species which share the character of having peduncles as thick as, or thicker than the subjacent internode. It is also quite common to find two umbelliform clusters of flowers upon the same peduncle, one terminal, the other lateral.

KEY TO THE SPECIES

- a. Corolla salverform, the tube definitely constricted; ovaries glabrous throughout; plants more or less glaucous throughout..... 2. *S. glaucum*
- aa. Corolla rotate-subcampanulate, the tube not definitely constricted; ovaries sericeous throughout or with densely sericeous styles; plants glabrescent to sericeous..... 3. *S. clausum*

2. SARCOSTEMMA GLAUCUM HBK. Nov. Gen. et Sp. Pl. 3:194. 1819, ex char. (T.: *Humboldt* & *Bonpland* s. n. in *Herb. Paris.*).

*Funastrum glaucum* (HBK). Schltr. in Fedde's Repert. 13:285. 1915.

*Philibertia ovalifolia* Rusby, Descr. So. Am. Pl. 94. 1915. (T.: *H. H. Smith* 1683 in *Herb. N. Y. Bot. Gard.*!).

*Funastrum ovalifolium* (Rusby) Killip, in Jour. Wash. Acad. Sci. 21:351. 1931.

Stems twining, gray-green, glabrous; lateral branches normally few. Leaves narrowly elliptic, oblong to ovate, acute, cuneate to obtuse, 5.0–7.5 cm. long, 0.5–3.0 cm. wide, subcoriaceous, revolute when dried, glaucous, glabrous on both surfaces, with one or more glands on the midrib at the base; petiole 0.3–0.5 cm. long. Inflorescences umbelliform, 18- to 35-flowered; peduncle 0–7 cm. long, equalling the subjacent internode in thickness, often bearing two catenulate cymes, glabrous; bracts linear, minute; pedicels 1–2 cm. long, glabrous. Calyx lobes ovate, 1.5 mm. long, glabrate on both surfaces, ciliolate; squamellae absent. Corolla salverform, white, the tube 2 mm. long, constricted, the lobes ovate, obtuse, 4–6 mm. long, puberulous-papillate on both surfaces, ciliolate. Gynostegium 2 mm. high, the column about 0.5–1.0 mm. long. Anthers 1.5 mm. long, the apical appendage deltoid, the pollinium-sacs oblongoid, somewhat flattened, 0.75 mm. long, with ellipsoid-sagittate corpusculum; ring of the corona prominent, revolute, adnate to the base of the corona vesicles; vesicles of the corona ovoid, pointed at the tip, 1.5–2.0 mm. long. Ovaries 3 mm. long, glabrous; stigma-head conical, obscurely 2-fid. Follicles narrowly obclavate-fusiform, 8.5 cm. long, 1 cm. thick,



glabrous; seeds flattened, 6 mm. long, 4 mm. wide, minutely papillate on both surfaces, the margin thin and serrate apically; coma about 2.5 cm. long.

This species often is confused with *S. clausum*, but although the two are alike superficially, there are a number of characters to separate them. One of the best is the fact that the corolla tube is constricted in *S. glaucum*, while the flowers are somewhat smaller and more abundantly produced. As the specific name suggests, *S. glaucum* has a characteristic glaucous aspect throughout. The doubled inflorescence also is more common in this species, where the peduncle sometimes is absent.

*Philibertella ovalifolia* Rusby was described for a variant with leaves wider than those of the typical form, but the two sorts occur in the same area and merge with one another. Although *S. glaucum* appears to be fairly common, only one specimen with fruit has been seen.

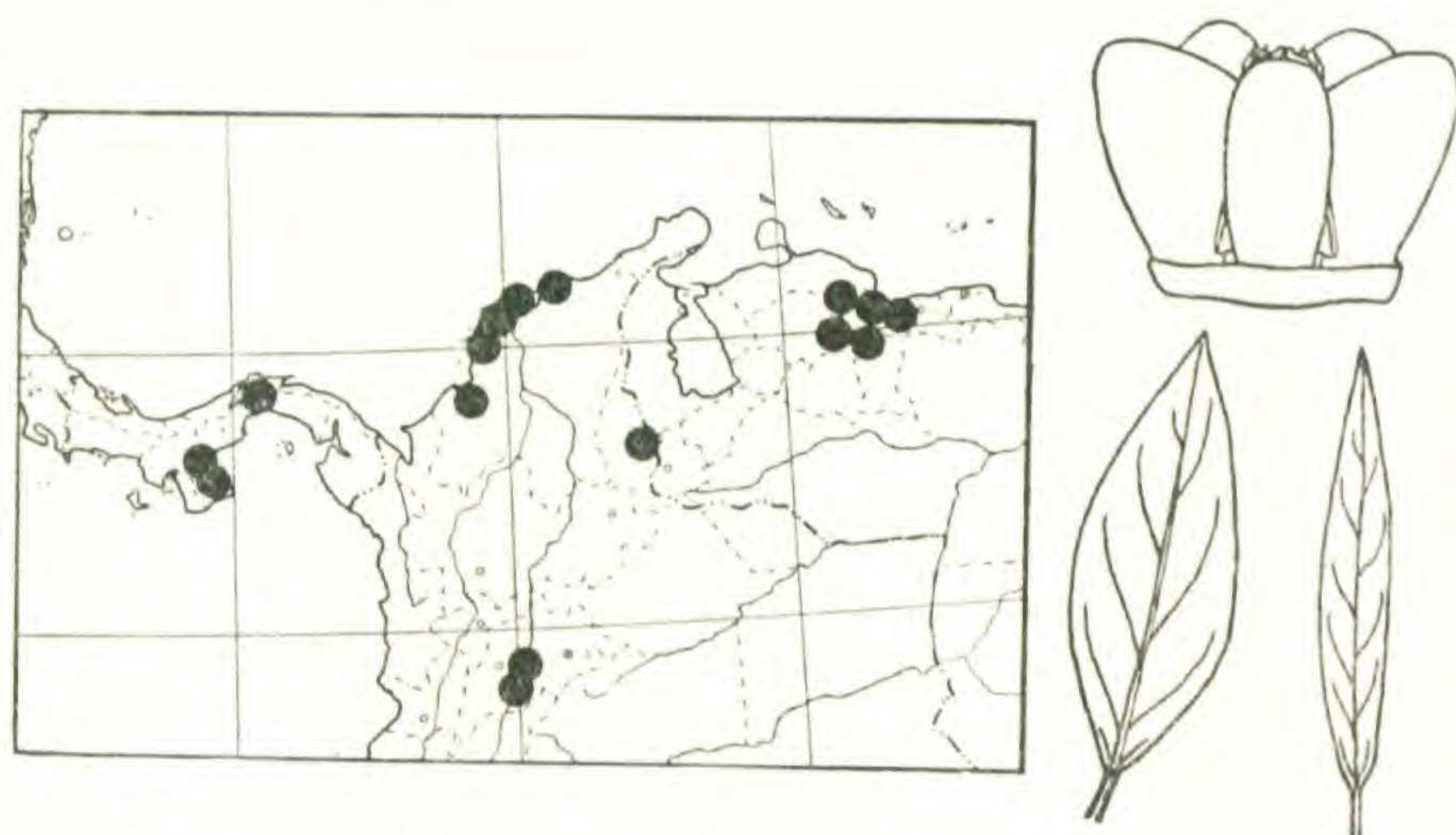


Fig. 6. Distribution, gynostegium, and leaves of *S. glaucum*.

*Sarcostemma glaucum* has been collected in Panama, Venezuela, and Colombia, where it grows along the coast, both in marshy and arid thickets or forest margins. The maximum recorded altitude attained by the species is 2500 feet, but it appears to be more common near sea level. Flowering specimens are dated from July 19 to March 6.

PANAMA. COCLÉ: Aguadulce, *Pittier* 4977. HERRERA: near Chitré, *Allen* 1090. PANAMA: Juan Díaz, *Standley* 30510.

COLOMBIA. ATLÁNTICO: Ponedera, *Dugand* & *Jaramillo* 2750; between Palmar de Varela & Ponedera, *Dugand* 3658; Puerto Giraldo, *Dugand* & *Jaramillo* 4187. BOLIVAR: Cartagena, *E. Martínez* 83, *Heriberto* 288; Barranquilla, *Elias* 441, *Dugand* 102; Los Volcánes, near Turbaco, *Killip* & *Smith* 21111, 14323; S of Mawatoca, *H. H. Smith* 2779; Sincelejo, *Pennell* 4058. CUNDINAMARCA: Girardot, *Rusby* & *Pennell* 76; Hacienda El Cucharo, between Tocaima & Pubenza, *Killip*, *Dugand* & *Jaramillo* 38922. HUILA: quebrada de Ángeles to Río Cabrera, *Rusby* & *Pennell* 342. MAGDALENA: Santa Marta, *H. H. Smith* 1682, 2524, *Killip* & *Smith* 21105. SANTANDER DEL NORTE: Cúcuta, *Killip* & *Smith* 20999.

VENEZUELA. ARAGUA: La Trinidad de Maracay, *Pittier* 5783. CARABOBO: near Valencia, *Pittier* 9429; near Trincheras, near Valencia, *Pittier* 7653. LARA: Barquisimeto, *Santiago* 60. PORTUGUESA: near Acarigua, *L. Williams* 12460. ZULIA: near Perijá, *Tejera* 201, 225.

PERU. data incomplete, *Maclean* s. n.



3. *SARCOSTEMMA CLAUSUM* (Jacq.) Roem. & Schult. Syst. Veg. 6:116. 1820.*Cynanchum clausum* Jacq. Select. Stirp. Amer. 1:87, t. 60. 1763.*Asclepias viminalis* Sw. Prodr. 53. 1788.*Sarcostemma Brownei* G. F. Meyer, Prim. Fl. Esseq. 139. 1818.*Sarcostemma cumanense* HBK. Nov. Gen. et Sp. Pl. 3:195. 1819, ex char. (T.: *Humboldt* & *Bonpland* s. n. in *Herb. Paris.*).*Sarcostemma pubescens* HBK. loc. cit. 194. 1819, ex char. (T.: *Humboldt* & *Bonpland* s. n. in *Herb. Paris.*).*Sarcostemma Swartzianum* Schult. Syst. Veg. 6:116. 1820.*Sarcostemma lineare* Spreng. Neue Entd. 3:35. 1822, non Decne.*Sarcostemma bonariense* Hook. & Arn. in Hook. Lond. Jour. Bot. 1:296. 1834, ex char. (T.: *Tweedie* s. n. in *Herb. Kew.*).*Sarcostemma apiculatum* Decne. in DC. Prodr. 8:539. 1844, ex char. (T.: *Gardner* 819 in *Herb. Delessert.*).*Sarcostemma crassifolium* Decne. loc. cit. 540. 1844, ex char. (T.: *Galeotti* 1529 in *Herb. Paris.*).*Sarcostemma Dombeyanum* Decne. loc. cit. 539. 1844. (T.: *Dombey* s. n. in *Herb. Paris!*).*Sarcostemma riparium* Decne. loc. cit. 540. 1844, ex char. (T.: in *Herb. Paris.*).*Philibertia viminalis* (Sw.) A. Gray, in Proc. Amer. Acad. 12:64. 1877.*Philibertia crassifolia* (Decne.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:318. 1881.*Philibertia cumanensis* (HBK.) Hemsl. loc. cit. 1881.*Sarcostemma barbatum* Mart. ex Fourn. in Mart. Fl. Bras. 6<sup>4</sup>:235. 1885, ex char. (T.: *Martius* s. n.).*Sarcostemma bifidum* Fourn. loc. cit. 234. 1885, ex char. (T.: *Mikan* I in *Herb. Vindobon.*).*Sarcostemma cuspidatum* Fourn. loc. cit. 233. 1885, ex char. (T.: *Poeppig* 2923 in *Herb. Vindobon.*).*Sarcostemma Gardneri* Fourn. loc. cit. 1885, ex char. (T.: *Gardner* 1357).*Sarcostemma pallidum* Fourn. loc. cit. 235. 1885, ex char. (T.: *St. Hilaire* Cat. C<sup>2</sup> 1489).*Sarcostemma pedunculatum* Fourn. loc. cit. 1885, ex char. (T.: *Glaziov* 8168 in *Herb. Paris.*).*Sarcostemma Schottii* Fourn. loc. cit. 234. 1885, ex char. (T.: *Pohl* & *Schott* 5381 in *Herb. Vindobon.*).*Philibertia Palmeri* A. Gray, in Proc. Amer. Acad. 21:394. 1886. (T.: *Palmer* 5 in *Herb. Gray!*).*Philibertia clausa* (Jacq.) K. Schum. in E. & P. Nat. Pflanzenfam. 4<sup>2</sup>:229. 1895.*Philibertia Gardneri* (Fourn.) K. Schum. loc. cit. 1895.*Philibertella clausa* (Jacq.) Vail, in Bull. Torr. Bot. Club 24:306. 1897.*Philibertella crassifolia* (Decne.) Vail, loc. cit. 1897.*Philibertella cumanensis* (HBK.) Vail, loc. cit. 1897.*Philibertella Palmeri* Vail, loc. cit. 1897.*Sarcostemma Glaziovii* K. Schum. in Engl. Bot. Jahrb. 25, Beibl. 60:19. 1898, ex char. (T.: *Glaziov* 21744 in *Herb. Berol.*).*Philibertia bonariensis* (H. & A.) Malme, in Sv. Vet. Akad. Afh. 34:23. 1900.*Philibertia cuspidata* (Fourn.) Malme, loc. cit. 24. 1900.*Philibertia riparia* (Decne.) Malme, in Bih. Sv. Akad. Vet. 27:7. 1901.*Philibertella lasiantha* Schltr. in Engl. Bot. Jahrb. 37:607. 1906, ex char. (T.: *Eggers* 14547 in *Herb. Berol.*).*Philibertella pallida* (Fourn.) Schltr. loc. cit. 1906.*Philibertella pedunculata* (Fourn.) Schltr. loc. cit. 1906.*Cynanchum mexicanum* T. S. Brandeg. in Univ. Calif. Publ. Bot. 4:380. 1913. (T.: *Purpus* 6017 in *Herb. Univ. Calif.*!).*Philibertella riparia* (Decne.) Stuntz, Invent., U. S. Bur. Pl. Ind. 31:87. 1914.*Funastrum apiculatum* (Decne.) Schltr. in Fedde's Repert. 13:283. 1915.*Funastrum barbatum* (Mart.) Schltr. loc. cit. 1915.



- Funastrum bonariense* (H. & A.) Schltr. loc. cit. 1915.  
*Funastrum clausum* (Jacq.) Schltr. loc. cit. 1915.  
*Funastrum crassifolium* (Decne.) Schltr. loc. cit. 1915.  
*Funastrum cumanense* (HBK.) Schltr. loc. cit. 1915.  
*Funastrum cuspidatum* (Fourn.) Schltr. loc. cit. 1915.  
*Funastrum Dombeyanum* (Decne.) Schltr. loc. cit. 1915.  
*Funastrum Gardneri* (Fourn.) Schltr. loc. cit. 1915.  
*Funastrum Glaziovii* (K. Sch.) Schltr. loc. cit. 1915.  
*Funastrum lasianthum* Schltr. loc. cit. 1915.  
*Funastrum pallidum* (Fourn.) Schltr. loc. cit. 1915.  
*Funastrum Palmeri* (A. Gray) Schltr. loc. cit. 1915.  
*Funastrum pedunculatum* (Fourn.) Schltr. loc. cit. 1915.  
*Funastrum pubescens* (HBK.) Schltr. loc. cit. 1915.  
*Funastrum riparium* (Decne.) Schltr. loc. cit. 1915.  
*Funastrum Schottii* (Fourn.) Schltr. loc. cit. 287. 1915.  
*Funastrum fragile* Rusby, in Mem. N. Y. Bot. Gard. 7:332. 1927. (T.: *White 2088* in *Herb. N. Y. Bot. Gard.*!).  
*Funastrum lanceolatum* Rusby, loc. cit. 1927. (T.: *M. Cardenas 2* in *Herb. N. Y. Bot. Gard.*!).  
*Funastrum Seibertii* Woods, in Ann. Mo. Bot. Gard. 24:199. 1937. (T.: *Seibert 637* in *Herb. Mo. Bot. Gard.*!).

Stems twining or trailing, gray-green, glabrous, the nodes densely white-pubescent; lateral branches normally few. Leaves frequently caducous, elliptic to oval, rarely much reduced, acuminate to mucronate, obtuse to shallowly cordate, 2–5 cm. long, 0.5–2.5 cm. wide, membranaceous to subcoriaceous, glabrate to sericeous above and beneath, with one or more glands on the midrib at the base; petiole 0.2–0.6 cm. long. Inflorescences umbelliform, rarely with two catenulate cymes, 7- to 15-flowered; peduncle stout, usually equalling the subjacent internode in thickness, 3.5–6.0 cm. long, glabrate to sericeous; bracts linear, minute; pedicels 1.5–2.5 cm. long, glabrate to puberulent. Calyx lobes ovate, 3–4 mm. long, densely puberulent without, glabrate within; squamellae alternate, paired or solitary. Corolla rotate-subcampanulate, pale greenish yellow to white, the tube 2.5 mm. long, not definitely constricted, the lobes ovate-elliptic, acute, 6–9 mm. long, densely puberulent without, glabrate to minutely puberulent within, ciliolate. Gynostegium 3 mm. high, the column short, about 0.5 mm. long. Anthers 1.5 mm. long, the apical appendage reniform to orbicular, the pollinium-sacs cylindrical-oblongoid, 1.8 mm. long, with sagittate corpusculum; ring of the corona prominent, revolute, adnate to the base of the corona vesicles; vesicles of the corona ovoid, pointed at the tip, 2.5 mm. long. Ovaries 2.5 mm. long, the styles sericeous, rarely sericeous throughout; stigma-head convex, with a short 2-fid apiculation. Follicles obclavate, attenuate, 5.0–8.5 cm. long, 1.2–1.5 cm. thick, puberulent, finely striate; seeds flattened, 4–6 mm. long, 2–3 mm. wide, minutely papillate on both surfaces, the margin thin and serrate apically; coma about 2 cm. long.

A species as bewilderingly variable as *Sarcostemma clausum* poses a serious question for the taxonomist. Although sufficiently common and variable to have developed a phenomenal synonymy, it is not sufficiently abundant in herbaria for analyses of variation to be made. Undoubtedly a species which ranges from southern United States to Argentina, which occupies both hydric and xeric habitats, and



which is insect-pollinated, will differentiate ecologic or geographic populations. Only very limited samples, often of a single plant, of these local groups are available to the botanist. In such a case, one alternative is to describe each specimen which is different in several aspects of morphology as new, in the hope that it eventually will be found to be a valid species. This is what has been done in the past with the majority of the Asclepiadaceae. The other alternative is to recognize that the specimen is slightly different in one, or perhaps several characters, but to refrain from describing it as a species until it can be proven to be a well-defined population which has achieved some measure of isolation from its cogeners.

After studying the some few hundred specimens collected from the entire range of *S. clausum*, I have come to the conclusion that there are essentially no significant differences, although the leaves are quite variable in shape, size, and pubescence, and the peduncles vary in size and thickness. The fact that these vegetative forms tend to occupy certain regions indicates that *S. clausum* probably has differentiated into several subspecific groups. It would be extremely dangerous to attempt to define the limits of such intergrading populations on the basis of a very few examples. I have followed, therefore, the alternative of recognizing only one species which eventually will perhaps be split into smaller groups.

*Sarcostemma clausum*, generally speaking, inhabits less arid habitats than most of the species of the genus. In Florida, Central America, and eastern South

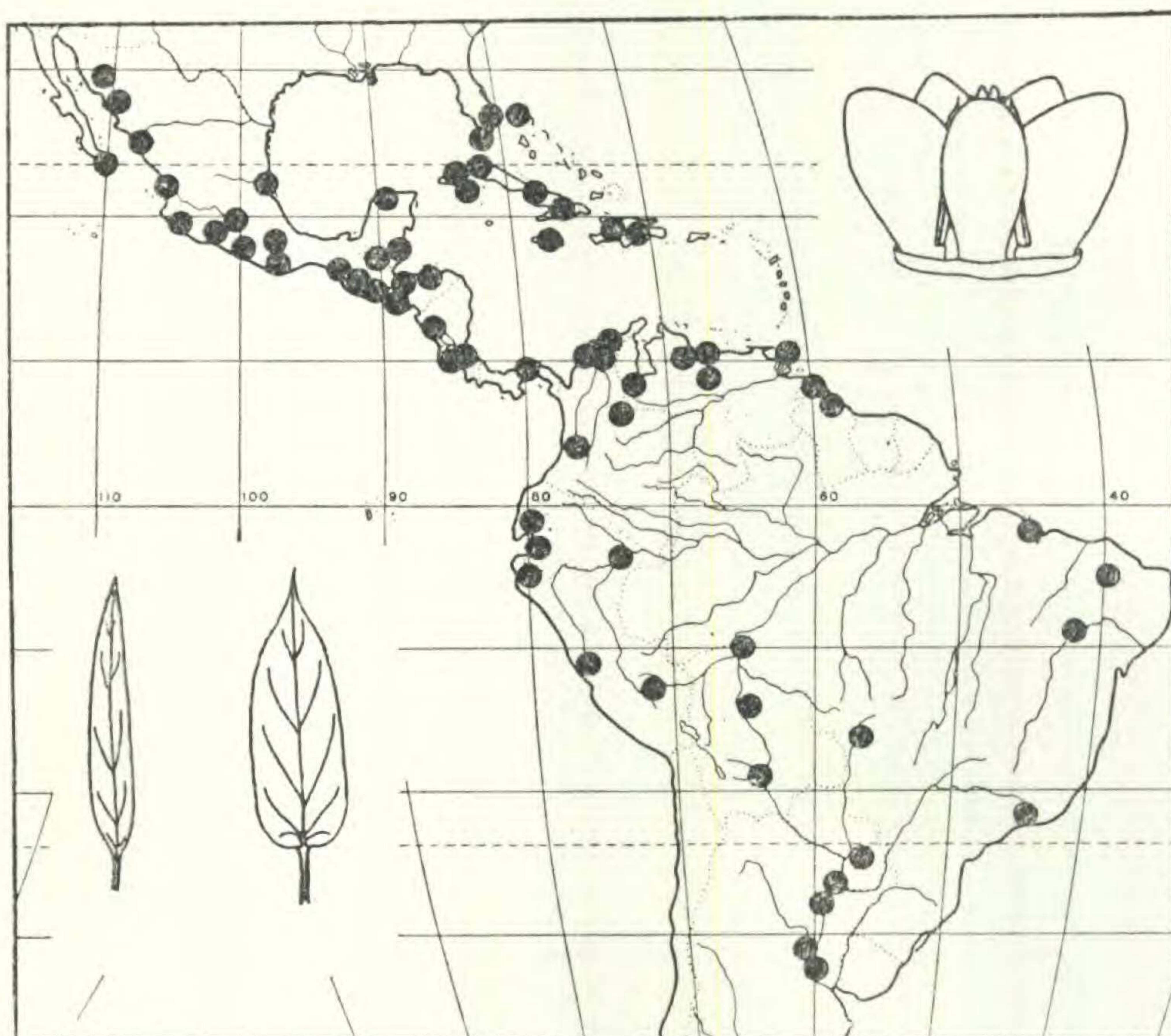


Fig. 7. Leaves, distribution, and gynostegium of *S. clausum*.



America, it is found on wooded slopes or in flood plains, or even growing in several feet of water. In Mexico and northwestern South America, on the other hand, it is commonest in sandy strand areas or savannas. The altitudinal range is from sea level to about 4000 feet. The plant apparently is in flower the year round through most of its range and has been described as "extremely fragrant, covered with masses of white flowers."

UNITED STATES. FLORIDA: DADE CO.: Miami, *Garber 11939*. LEE CO.: Fort Myers, *Hitchcock 207*. MONROE CO.: Fishbone Key, *Seibert 1337*; Big Pine Key, *Killip 3174*; Key West, *Curtiss 5624*; Bahia Honda Key, *Woodson & Schery 119*; Elliot's Key, *Small & Nash s. n.*

MEXICO. BAJA CALIFORNIA SUR: San José del Cabo, *T. S. Brandegee s. n.*; S of San José del Cabo, *Johansen 514*. CHIAPAS: Jalisco, *Purpus 9170*; Escuintla, *Matuda 0699*. CHIHUAHUA: SW Chihuahua, *E. Palmer 5*, type of *P. Palmeri* Gray. COLIMA: Manzanillo, *Ferris 6128*, *Palmer 1002*; Paso del Río, *Emrick 11*. GUERRERO: Baqueta, *Langlassé 508*; Guayameo, *Mina, Hinton 9370*; Actoyac, *Galeana, Hinton 14602*; Vallecitos, *Montes de Oca, Hinton 10607*; Pungarabato, *Coyuca, Hinton 6452*; NW of Acapulco, *Barkley 14103*. JALISCO: Bolaños, *Rose 2912*; Tenacatita Bay, *Elmore 1A23*. MICHOACAN: Coalcomán, *Aquila, Hinton 15833*. MORELOS: near Cuernavaca, *Pringle 7109*; Xochitepec, *Lyonnet 1037*. NAYARIT: Mexcaltitlán, *Mexia 1016*. OAXACA: near Tomellin, *Rose, Painter & Rose 10054*; near Cuicatlán, *E. W. Nelson 1615, 1680, L. C. Smith 249*; Chiltepec, *Tuxtepec, Martínez-Calderón 196*; San Antonio, *C. L. Smith 836, Pringle 4849*; Tomellin, *Olssen-Seffer s. n.*; Etlá, near Bocas del Ríos, *Seler & Seler 4852*. SINALOA: Culiacán, *T. Brandegee s. n.*; loc. unknown, *Ortega 4230*. SONORA: Hermosillo, *Drouet & Richards 3564*; 23 miles NE Ures, *Shreve 6732*; Río Mayo, *Gentry 2286*; near Batuc, *Wiggins & Rollins 454*; 25 miles from Ures, *Wiggins 7387*. TABASCO: Caño de Curahue, *Rovirosa 32*. TAMAULIPAS: Tampico, *E. Palmer 498*. VERA CRUZ: Pánuco River near Ebano, *Le Sueur 358*; loc. unknown, *Purpus 6017*, type of *C. mexicanum* Brandeg. YUCATAN: Progreso, *Flores 7*.

BRITISH HONDURAS: Corozal District, *Gentle 503, 807*; Honey Camp, *Lundell 517*; Santa Rita, *Gentle 73*; Northern River, *Gentle 883*.

GUATEMALA. ALTA VERAPAZ: Samac, *Johnson 776*; Pancajche, *Johnson 1017*. AMATITLÁN: Amatitlán, *von Tuerckheim 8710, J. D. Smith 2778, Morales 1136*; Lake Amatitlán, *Kellerman 4359, J. D. Smith 1940*. CHIQUIMULA: near Chiquimula, *Standley 73865*. ESCUINTLA: Río Guacalate, *Standley 58204, 60163*; San José, *Standley 63961, Hayes s. n.* GUATEMALA: near Lago de Amatitlán, *Standley 89433*. JUTIAPA: near Jutiapa, *Standley 75185*. IZABAL: Boca del Palochi, *J. D. Smith 1734*; NE of San Felipe, *Steyermark 39662*. PETÉN: S of Sayaxché, *Steyermark 46229*. RETALHULEU: near Retalhuleu, *Standley 88251, 88837*. SAN MARCOS: Ocos, *Steyermark 37820*; Río Suchiate, W of Ayutla, *Steyermark 38030*. SOLOLA: S-facing slopes, Volcán Atitlán, *Steyermark 48010*; Santa Barbara, *Shannon 169*. SANTA ROSA: Ríos de los Esclavos, *Heyde & Lux 4001*; Casillos, *Aquilar 303*; Agua Caliente, *Kellerman 7737*. SUCHUTEPEQUEZ: Río Najuala, *Shannon 399*. ZÁCAPA: Baños de Santa Marta, *Standley 73932*; Zácapa, *Deam 154, Kellerman 4359*.

EL SALVADOR. AHUACHAPÁN: loc. unknown, *Padilla 115*. SAN SALVADOR: along road from San Martín to Laguna de Ilopango, *Standley 22589*.

HONDURAS. ATLÁNTIDA: Tela, *Standley 54664*. CORTES: Río Lindo, *Edwards P-683*. SANTA BARBARA: San Pedro Sula, *Thieme 5342*. YORO: near Coyoles, Aguán Valley, *Yunker, Koepfer & Wagner 8122*.

NICARAGUA. GRANADA: Granada, *Grant 903*. MANAGUA: near Managua, *Garnier 1128*.

COSTA RICA. SAN JOSÉ: near El General, *Skutch 2171*. TALAMANCA: Delta de Turitkub, *Tonduz 8661*.

PANAMA. BOCAS DEL TORO: Changuinola River, *Dunlap 289*. CANAL ZONE: Barro Colorado Island, *Bangham 413, Kenoyer 501, Shattuck 315, 1114, Brown 155, Wilson 66, Bailey & Bailey 530*; near Empire, Culebra Cut, *Hunter & Allen 775*. PANAMÁ: swamp



between El Jagua Hunting Club on Río Jagua and El Condor Hill, *Hunter & Allen* 482; near Arenoso, lower Río Trinidad, *Seibert* 637.

CUBA. CAMAGUEY: Cayo Romano, *Shafer* 2494; Cayo Sabinal, Granada, *Shafer* 877. HAVANA: Laguna de Castellano, *P. Wilson* 9559; San Antonio, *Shafer* 247. ORIENTE: Ensenada de Mora, *Britton, Cowell & Shafer* 12960; near Nirua-Nirua, *Britton & Cowell* 12719; Bayamo, *Ekman* 7590; Río Jagua, *Ekman* 6653; *Wright* 1666. ISLA DE PINOS: Nueva Gerona, *Curtiss s. n.*; Don José, *Blain* 104. LAS VILLAS: Belmonte, Sóledad, Cienfuegos, *Jack* 7728, 6856, 5342; Cienfuegos, Cienquita, *Combs* 330; Ciénaga de Zapata, N of Bahía de Cochinas, *Leon & Soustalot* 8497; Gaviñon, vic. Sóledad, *Howard* 6298. PINAR DEL RÍO: near Mendoza, *Shafer* 10608; Laguna Jovera, *Shafer* 10983.

HISPANIOLA. HAITI: near Port au Prince, *Leonard* 10092; near Gros Morne, *Leonard* 9934, 9980; near Jean Rabel, *Leonard & Leonard* 12799; near Étang, *Leonard* 3570.

DOMINICAN REPUBLIC: Barahona, *Fuertes* 202, 1260; S of Monte Cristi, near Río Yaque del Norte, *Howard & Howard* 9569.

JAMAICA: Blue Mts., *Hitchcock s. n.*; Arntully, *Orcutt* 3111; Port Henderson, *Harris & Lawrence* C1536; Hope Bay, *Wight* 169; Kingston, *Brown* 379; below Cinchona, *Maxon & Killip* 1043.

BAHAMA ISLANDS: New Islands, *Britton & Brace* 482, 770; Great Bahama, *Brace* 3602, *Britton & Millsbaugh* 2661.

TRINIDAD: east of Icacos, *Cheesman & Baker* 388.

COLOMBIA. AMAZONAS: Río Putamayo, between Río Igara-Paraná and Río Yaguas, *Schultes* 3998. BOLÍVAR: Calamar, *Killip & Smith* 14708; near Turbaco, *Killip & Smith* 14437; Buenavista, east of Sincé, *Pennell* 3981; near Puerto Colombia, *Elias* 396. CAUCA: La Manuelita, Palmira, *Pittier* 787. EL VALLE: Espiñol, below Dagua, *Killip & Hazen* 11076; N of Palmire, *Garcia B.* 6408; "La Manuelita," *Pennell & Killip* 6191. HUILA: above Natagaima, *Rusby & Pennell* 270. MAGDALENA: Santa Marta, *H. H. Smith* 1681; Fonseca, *Haught* 4387; 15 miles N of Becerril, *Haught* 3694. SANTANDER: Puerto Wilches, *Killip & Smith* 14937. SANTANDER DEL NORTE: near Sarare, *Cuatrecasas* 13258; near Florida, *Killip & Smith* 16176. TOLIMA: Doima, *Haught* 2442; Mariquita, *Pennell* 3632.

ECUADOR. GUAYAS: Guayaquil, *Mille* 961, *Asplund* 5150. LOS RÍOS: Río Pita, *Asplund* 5588.

PERU. APURIMAC: Abancay, *Vargas* 750. LIMA: Hacienda Peramango, Río Pativilea Valley, *Seibert* 2313; Chosica, *Macbride & Featherstone* 535. LORETO: Iquitos, Creek Itaya, *Mexia* 6482. PIURA: Huancabamba, *Serran*, *Stork* 11387; Negritos, *Haught* F-49; Pariñas Valley, *Haught* 145, *Spruce* 6486. TUMBES: Tumbes, mts. SE Hacienda La Choza, *Weberbauer* 7694.

VENEZUELA. ARAGUA: Maracay, El Limón, *Pittier* 10102; potreros de Las Delicias, *Lasser* 860. DISTRITO FEDERAL: Bajo Cotiza, *Vogl* 458; near Caracas, *Eggers* 13121, *Pittier* 7583. GUARICO: El Sombrero, *Pittier* 13557. FALCON: Meachiche, *Lasser* 186. MÉRIDA: Tovar, *Fendler* 1054. YARACUY: near Guama, *Pittier* 11163.

BRITISH GUIANA: Vreed-en-Hoop, *Hitchcock* 16738; Morawhanna, *Hitchcock* 17511; Parika, *Hitchcock* 16754; east coast, *Persaud* 302.

SURINAM: *Hostmann* 962.

BRAZIL. CEARÁ: Carupe, *Drouet* 2619; Río de Janeiro, *Glaziou* 8168, *Dusén* 1968. MATTO GROSSO: Cuyabá, *Malme* 3247, *Hoehne* 25072; Santa Cruz de Parra, *Lindman* A2853. PARÁ: 2 km. S Baião, *Drouet* 1992. RIO DE JANEIRO: Isla Paqueta, *Dusén* 5.

BOLIVIA. SANTA CRUZ: Portachuelo, *Steinbach* 3235; W of Río Parai, *Herzog* 1362; Río Ibon, *O. E. White* 2088, type of *F. fragile* *Rusby*.

PARAGUAY: Asunción, *Morong* 681, *Malme s. n.*; Carapeguá, *Rojas* 3220; Ypacaray, *Hassler* 72118; Pilcomayo River, *Morong* 1526; Laguna Ypacaray, *Fiebrig* 331, *Hassler* 12118; Santa Elisa, *Hassler* 2760; between Río Apa and Río Aquidaban, *Fiebrig* 4250.

ARGENTINA. CHACO: Fontana, *T. Meyer* 215; La Fidelidad, *Jørgensen* 3037. FORMOSA: Formosa, *Jørgensen* 1918, 2606; Gubernación Formosa, *Kermes* 380. JUJUY: San Pedro de Jujuy, *Schreiter* 5207. SALTA: Orán, *Schreiter* 33559, 10842; Embaración, *Schreiter* 5227. SANTA FE: Los Amores, General Obligado, *Ragonesi* 3235.



## Series 3. CYNANCHOIDES R. Holm, ser. nov.

Inflorescentia ut videtur lateralis umbelliformis, cyma una, pedunculo quam internodio subjacenti angustiore (interdum obsoleto).

Type species: *Sarcostemma cynanchoides* Decne.

This largest series of the subgenus CERAMANTHUS includes those species which have lateral inflorescences borne upon peduncles not equalling the subjacent internode in thickness. They represent an apparently natural group which, however, is further divisible into groups of closely related species. These subdivisions have not been recognized nomenclaturally, but their relationships are discussed in connection with the particular species which they include, and are also expressed in the key.

## KEY TO THE SPECIES

- a. Leaves very broadly ovate-cordate to orbicular, the base cordate with converging lobes.
  - b. Petals strongly reflexed at maturity; ring of the corona relatively long and conspicuous; column nearly equalling the corona vesicles in length; corona vesicles ovoid to pyramidal. Plants of Mexico, Central America, and northeastern South America..... 4. *S. bilobum*
  - bb. Petals not reflexed at maturity; ring of the corona relatively short; column nearly obsolete; corona vesicles ovoid; leaves long-mucronate, conspicuously paler beneath. Plants of Guatemala..... 5. *S. odoratum*
- aa. Leaves broadly to narrowly lanceolate, the base usually cordate with descending or diverging lobes, obtuse or cuneate in very narrow leaves.
  - b. Petals strongly reflexed at maturity; leaves long, linear. Plants of South America..... 6. *S. gracile*
  - bb. Petals not strongly reflexed at maturity; leaves lanceolate to linear. Plants of North America.
    - c. Column exceeding the corona vesicles in length; vesicles of the corona constricted at their insertion upon the column; leaves very long, narrowly lanceolate, the margin usually undulate-crispate; follicles very attenuate..... 7. *S. crispum*
    - cc. Column shorter than the corona vesicles; vesicles of the corona not constricted at their insertion upon the column; leaves lanceolate to linear, the margin not undulate-crispate.
      - d. Corolla segments more than 6.5 mm. long, sepals more than 3.5 mm. long; leaves broadly lanceolate, the base cordate with descending lobes (rarely diverging or converging); relatively stout vines with few lateral branches. Plants of Texas and Mexico.
        - e. Column relatively long; stigma-head apiculate; leaves about twice as long as broad; peduncle usually shorter than the subtending leaves or obsolete. Plants of central Mexico..... 8. *S. elegans*
        - ee. Column relatively short; stigma-head obscurely bilobed; leaves about three or more times as long as broad; peduncle usually exceeding the subtending leaves. Plants of Texas and northern Mexico..... 9. *S. Torreyi*
      - dd. Corolla lobes less than 6.5 mm. long, sepals less than 3 mm. long; leaves lanceolate to linear, the base cordate with diverging (rarely descending or converging) lobes, or obtuse to cuneate.
        - e. Leaves broadly lanceolate to linear, the base cordate or hastate (rarely obtuse); ring of the corona free from the corona vesicles..... 10. *S. cynanchoides*
        - ee. Leaves narrowly lanceolate to linear or oblanceolate, the base obtuse to cuneate; ring of the corona adnate to the base of the corona vesicles.







basis of slight differences, chiefly in pubescence, and the names *S. odoratum* and *S. elegans* have been misapplied to these plants. Considering the problem as a whole I have been unable to distinguish more than one species, which is quite distinct from the true *S. odoratum*. At least two infraspecific entities are present, however, and their intergradation and enigmatic distribution still leave the taxonomy in an unsettled state. I have recognized two subspecies separated by the characters given in the key, together with other less tangible differences. *Sarcostemma b. bilobum* occurs, chiefly to the north and west, in Central America and southern Mexico. The putative hybrids have been designated as such since they do not appear to be part of a cline. Ecological data are sadly lacking; if available, they might explain the peculiar distribution of the subspecies. *Sarcostemma b. bilobum* apparently grows in open woods from 3000 to 9000 feet, and flowers from October to December.

MEXICO. CHIAPAS: between Teneapa and Yajalon, *E. W. Nelson* 3265; near Yajalon, *E. W. Nelson* 3412. COLIMA: Paso del Río, *Emrick* 178. JALISCO: Santa Cruz de Vallarta, *Mexia* 1271. MEXICO: Temascáltepec, *Hinton* 8473. MICHOACÁN: Coalcomán, Coahuayana, *Hinton* 16249. MORELOS: near Cuernavaca, *Pringle* 11887. OAXACA: Capital Concordia, *Reko* 3513; near Tehuantepec?, *Seler & Seler* 1790. YUCATÁN: Izamál, *Gaumer* 880 (in part).

GUATEMALA. PETÉN: Uaxactun, *Bartlett* 12470. SACATEPEQUEZ: Santiago, *Gomez* 787, type of *P. refracta* Donn. Sm.

HONDURAS. MORAZAN: Río El Quebracho above Jicarito, *Standley* 14814, type of *S. bellum* Standl. & L. Wms.

BRITISH HONDURAS: Honey Camp, *Lundell* LP33, 609.

PUTATIVE HYBRIDS: listed following *S. bilobum Lindenianum* (4b).

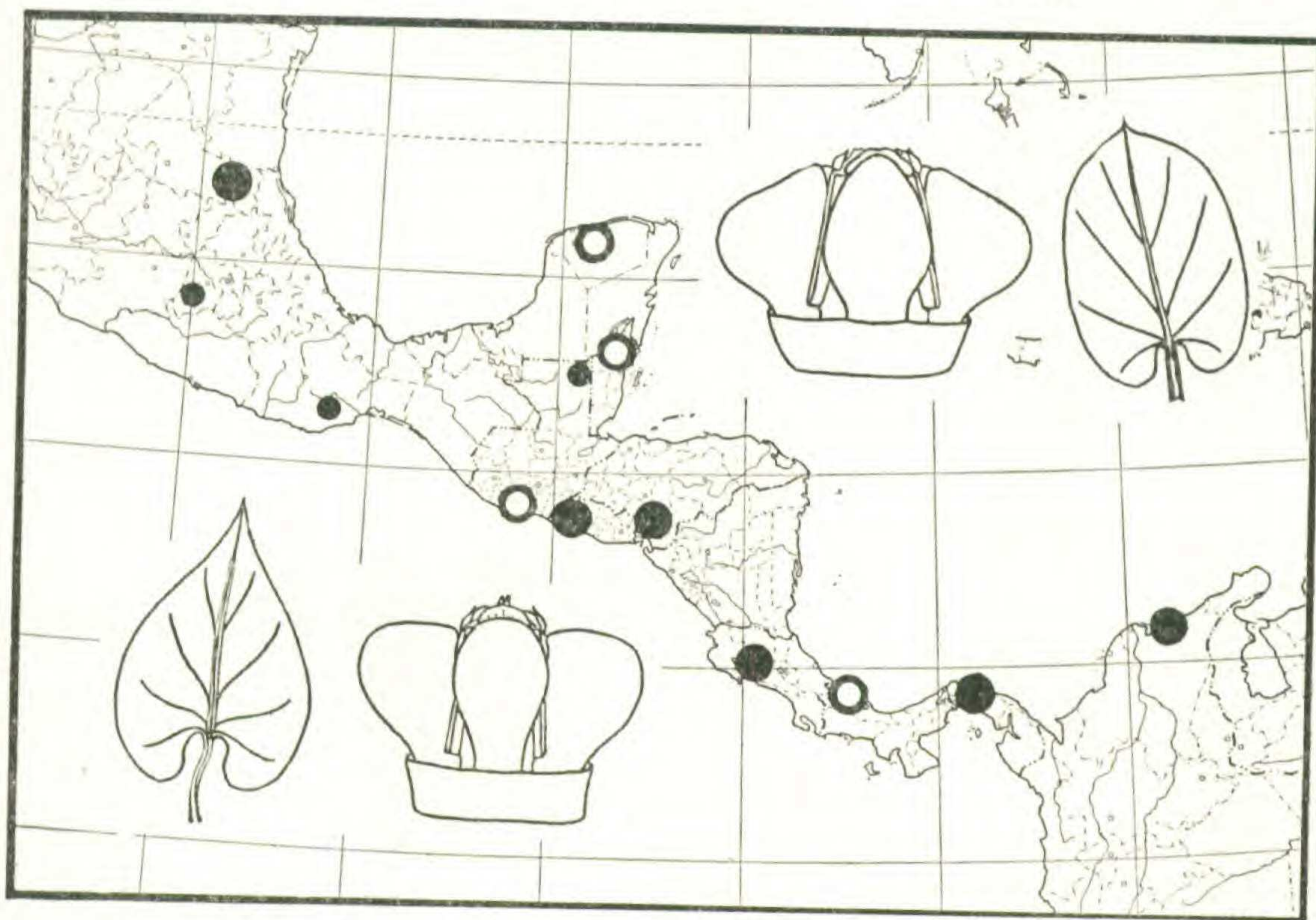


Fig. 8. Gynostegium and leaf of *S. bilobum bilobum* (lower left), of *S. bilobum Lindenianum* (upper right); distribution of *S. bilobum bilobum* (small dots), of *S. bilobum Lindenianum* (large dots), of putative hybrids, black circles.



- 4b. *SARCOSTEMMA BILOBUM* Hook. & Arn. ssp. **Lindenianum** (Decne.) R. Holm, stat. nov.

*Sarcostemma Lindenianum* Decne. in DC. Prodr. 8:541. 1844. (T.: *Linden s. n. in Herb. Paris!*).

*Philibertia Lindeniana* (Decne.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:318. 1881.

*Philibertia Ervendbergii* A. Gray, in Proc. Amer. Acad. 21:395. 1886. (T.: *Ervendberg 174 in Herb. Gray!*).

*Philibertia Fendleri* A. Gray, loc. cit. 1886. (T.: *Fendler 2119 in Herb. Gray!*).

*Philibertia reflexa* Pittier, in Contr. U. S. Nat. Herb. 13:96. 1910. (T.: *Pittier s. n. in U. S. Nat. Herb.!*).

*Philibertia dumetorum* T. S. Brandeg. in Univ. Calif. Publ. Bot. 4:380. 1913. (T.: *Purpus 6013 in Herb. Univ. Calif.!*).

*Funastrum Ervendbergii* (Gray) Schltr. in Fedde's Repert. 13:285. 1915.

*Funastrum Fendleri* (Gray) Schltr. loc. cit. 1915.

*Funastrum Lindenianum* (Decne.) Schltr. loc. cit. 286. 1915.

*Funastrum reflexum* (Pittier) Schltr. loc. cit. 287. 1915.

*Philibertia filipes* Rusby, Descr. S. Am. Pl. 94. 1920. (T.: *H. H. Smith 1669 in Herb. N. Y. Bot. Gard.!*).

*Funastrum dumetorum* (Brandeg.) Standl. in Contr. U. S. Nat. Herb. 23:1172. 1924.

Stems trailing or twining, gray-green, pilosulose; lateral branches normally few. Leaves oblong-orbicular, mucronate, deeply cordate, the lobes usually converging, 2–5 cm. long, 1.5–4.0 cm. wide, subcoriaceous, densely pilosulose on both surfaces, rarely glabrous, with one or more glands on the midrib at the base; petiole 1.0–2.5 cm. long. Inflorescences umbelliform, 7- to 10-flowered; peduncle 1.5–2.0 cm. long, subpilose; bracts usually linear, minute, occasionally foliaceous and ovate; pedicels 1–2 cm. long, subpilosulose. Calyx lobes linear to ovate, 2.5 mm. long, pilosulose without, glabrate within; squamellae usually solitary. Corolla rotate-subcampanulate, whitish with a median purple streak on each lobe, the tube 2 mm. long, the lobes reflexed at maturity, lanceolate, obtuse, 5.5 mm. long, glabrescent without, appressed-pilosulose within, ciliolate. Gynostegium 4 mm. high the column 1.5 mm. long. Anthers 1.5 mm. long, the apical appendage reniform, emarginate, the pollinium-sacs quadrate-oblongoid, somewhat flattened, 0.8 mm. long, with broadly sagittate corpusculum; ring of the corona thick, revolute, not adnate to the base of the corona vesicles; vesicles of the corona pyramidal, widest below the middle, 2 mm. long. Ovaries 2 mm. long, glabrous; stigma-head abruptly 2-apiculate to umbonate. Follicles obclavate, attenuate, 7 cm. long, 2 cm. thick, puberulent, finely striate; seeds somewhat flattened, 7 mm. long, 4 mm. wide, minutely papillate on both surfaces; coma about 3 cm. long.

The relationship of this subspecies with *S. b. bilobum* has been described in the discussion of the latter. *Sarcostemma b. Lindenianum* occurs, roughly to the south and east, in Mexico and Central America and extends into Colombia and Venezuela. The few data available indicate that it is found at much lower altitudes, from 50 to 80 feet above sea level, and blooms from July to September. Thus the isolating mechanisms may be in part ecological. I believe that mechanical difficulties attendant with hybridization also play an important part, in view of the differences in the pollinia.



MEXICO. CHIAPAS: Tonalá, *Purpus* 6651. SAN LUIS POTOSÍ: Rascón, *Purpus* 5494, 5256. VERA CRUZ: Acasonica, *Purpus* 8412; Baños del Corizál, *Purpus* 6013, type of *P. dumetorum* Brandeg.; Wartenburg, near Tantoyuca, *Ervendberg* 174, type of *P. Ervendbergii* Gray. YUCATÁN: Izamál, *Gaumer* 880 (in part).

HONDURAS. VALLE: San Lorenzo, *Rodriguez* 3486, 3331.

EL SALVADOR: Acajutla, *Calderón* 1676.

COSTA RICA: near San Mateo, *Biolley* 7095; Nicoya, *Pittier* s. n., type of *P. reflexa* Pittier; vic. Cascajal, 25 km. ESE of Puntarenas, *Holm & Iltis* 272.

PANAMA. PANAMA: banks of Mamoni River, above Chepo, *Pittier* 4728.

COLOMBIA. MAGDALENA: Santa Marta, *H. H. Smith* 1669, type of *P. filipes* Rusby.

VENEZUELA. MÉRIDA: Tovar, *Fendler* 2119, type of *P. Fendleri* Gray.

PUTATIVE HYBRIDS. MEXICO. YUCATÁN: Izamál, *Gaumer* 880 (in part). PANAMA. BOCAS DEL TORO: near Chiriquí Lagoon, *Wedel* 1755. GUATEMALA. ESCUINTLA: Santa Lucía, *Heyde & Lux* 47, 6353. BRITISH HONDURAS: Corozál District, Santa Rita, *Gentle* 829; San Andrés, *Gentle* 553.

5. *SARCOSTEMMA odoratum* (Hemsl.) R. Holm, comb. nov.

*Philibertia odorata* Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:319. 1881. (T.: *Salvin* s. n. in *Herb. Kew.*!).

*Funastrum odoratum* (Hemsl.) Schltr. in Fedde's Repert. 13:286. 1915.

Stems twining, gray-green, pilosulose to pilose; lateral branches normally few. Leaves narrowly to broadly ovate, long-mucronate, deeply cordate, the lobes converging, 3.5–5.0 cm. long, 2.0–4.5 cm. wide, subcoriaceous, pilosulose above, densely puberulous-pilose beneath, with one or more glands on the midrib at the base; petiole 2.5–4.0 cm. long. Inflorescences umbelliform, 6- to 12-flowered; peduncle 1.5–3.0 cm. long, pilosulose; bracts linear, minute; pedicels 1.5–2.0 cm. long, pilosulose. Calyx lobes narrowly lanceolate, 4 mm. long, subpilose without, glabrous within; squamellae usually solitary. Corolla rotate-subcampanulate, white, the tube 1 mm. long, the lobes ovate, 5 mm. long, pilosulose without, puberulous-papillate within. Gynostegium 2.5 mm. high, the column nearly obsolete. Anthers 1.5 mm. long, the apical appendage deltoid, the pollinium-sacs cylindrical, 0.75 mm. long, with sagittate corpusculum; ring of the corona thick, revolute, scarcely adnate to the base of the corona segments; vesicles of the corona ovoid, 2 mm. long. Ovaries 1.5 mm. long, glabrous; stigma-head abruptly 2-apiculate. Follicles and seeds unknown.

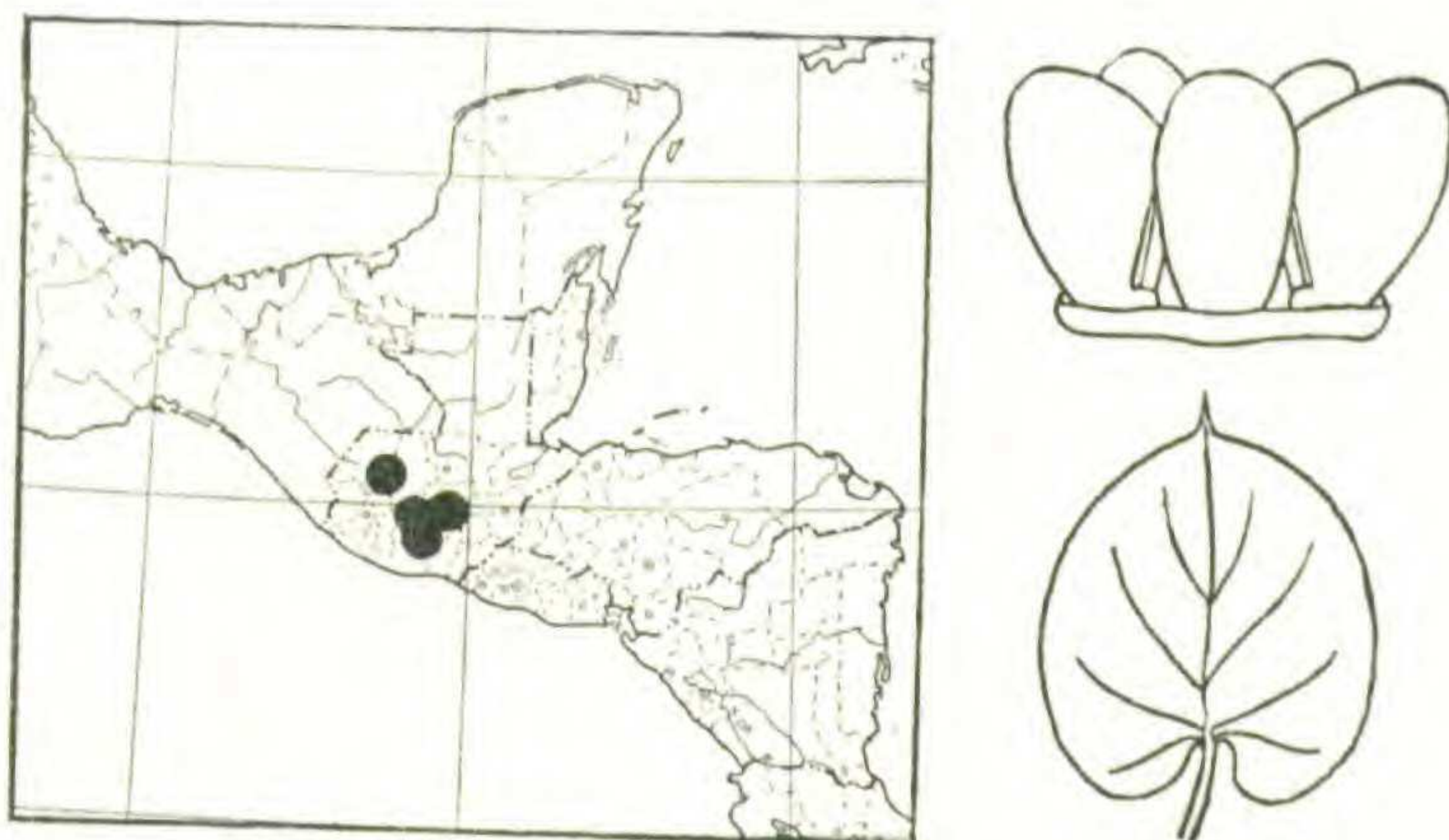


Fig. 9. Distribution, gynostegium and leaf of *S. odoratum*.



*Sarcostemma odoratum* is a rare species known only from Guatemala. The converging basal lobes of the leaves and characters of the gynostegium ally it with *S. bilobum*; it lacks the long column and reflexed corolla lobes of that species, however. It has been collected on hillsides from 4000 to 5000 feet; apparently it flowers from August to September.

GUATEMALA. CHIMALTENANGO: Chimaltenango, J. R. Johnston 752. GUATEMALA: Aguilar 313. HUEHUETENANGO: between San Sebastian H. and large peñasco above town, Steyermark 50514. SACATEPEQUEZ: Volcán de Fuego, Salvin s. n., type of *P. odorata* Hemsl. DATA INCOMPLETE: Brenas, Tonduz 785.

6. *SARCOSTEMMA GRACILE* Decne. in DC. Prodr. 8:539. 1844. (T.: Tweedie 1837 in *Herb. Kew.*!).

*Amphistelma exsertum* Griseb. Symb. Fl. Arg. 229. 1879, ex char. (T.: Lorentz & Hieronymous 1125).

*Sarcostemma carpophylloides* Morong, Enum. Pl. Paraguay (Ann. N. Y. Acad. Sci. 7:) 165. 1893. (T.: Morong 1004 in *Herb. N. Y. Bot. Gard.*!).

*Philibertia exserta* (Griseb.) Schltr. in O. Ktze. Rev. Gen. 3:200. 1898.

*Ceramanthus gracilis* (Decne.) Malme, in Ark. Bot. 4<sup>14</sup>:2. 1905.

*Funastrum gracile* (Decne.) Schltr. in Fedde's Repert. 13:285. 1915.

Stems twining, green, glabrous, the nodes puberulent; lateral branches many. Leaves narrowly lanceolate or linear, acute to acuminate, obtuse to cuneate, involute proximally 1–2 mm., 3.0–5.5 mm. long, 0.2–0.5 cm. wide, membranaceous, glabrate to minutely puberulent above and beneath, with no glands on the midrib at the base; petiole 0.1 cm. long. Inflorescences umbelliform, 8- to 16-flowered; peduncle 3.5–7.0 cm. long, glabrate to very minutely puberulent; bracts linear, minute; pedicels 0.9–1.5 cm. long, pilosulose. Calyx lobes lanceolate, 1.5 mm. long, minutely pubescent without, glabrous within; squamellae absent. Corolla rotate-subcampanulate, white, the tube 1 mm. long, the lobes reflexed, ovate, acute, 3.5 mm. long, glabrate without, minutely papillate within ciliolate. Gynostegium 2 mm. high, the column 1.5 mm. long. Anthers 1 mm. long, the apical appendage reniform, the pollinium-sacs oblongoid-cylindrical, 0.75 mm. long with sagittate corpusculum; ring of the corona thick, adnate to the base of the corona vesicles, vesicles of the corona ovoid, pointed at the tip, 1.5 mm. long. Ovaries 1.5 mm. long, essentially glabrous; stigma-head conical, obscurely 2-lobed. Follicles narrowly fusiform, 3.5–5.5 cm. long, 0.4–0.5 cm. thick, minutely puberulent; seeds somewhat flattened, 4 mm. long, 1.5 mm. wide, the margin flat and obscurely serrate; coma about 1 cm. long.

The small flowers with reflexed corolla lobes and the linear leaves separate this species at once from all other South American forms. Since it is distant from any species remotely resembling it, I hesitate to speculate as to its affinities. There is something reminiscent of *S. glaucum* in the floral structure and inflorescence, but the species hardly can be referred to series CLAUSA since the peduncle does not equal the stem in thickness and only rarely bears two cymes. This species may represent an extreme modification of the ancestral form of series CLAUSA.



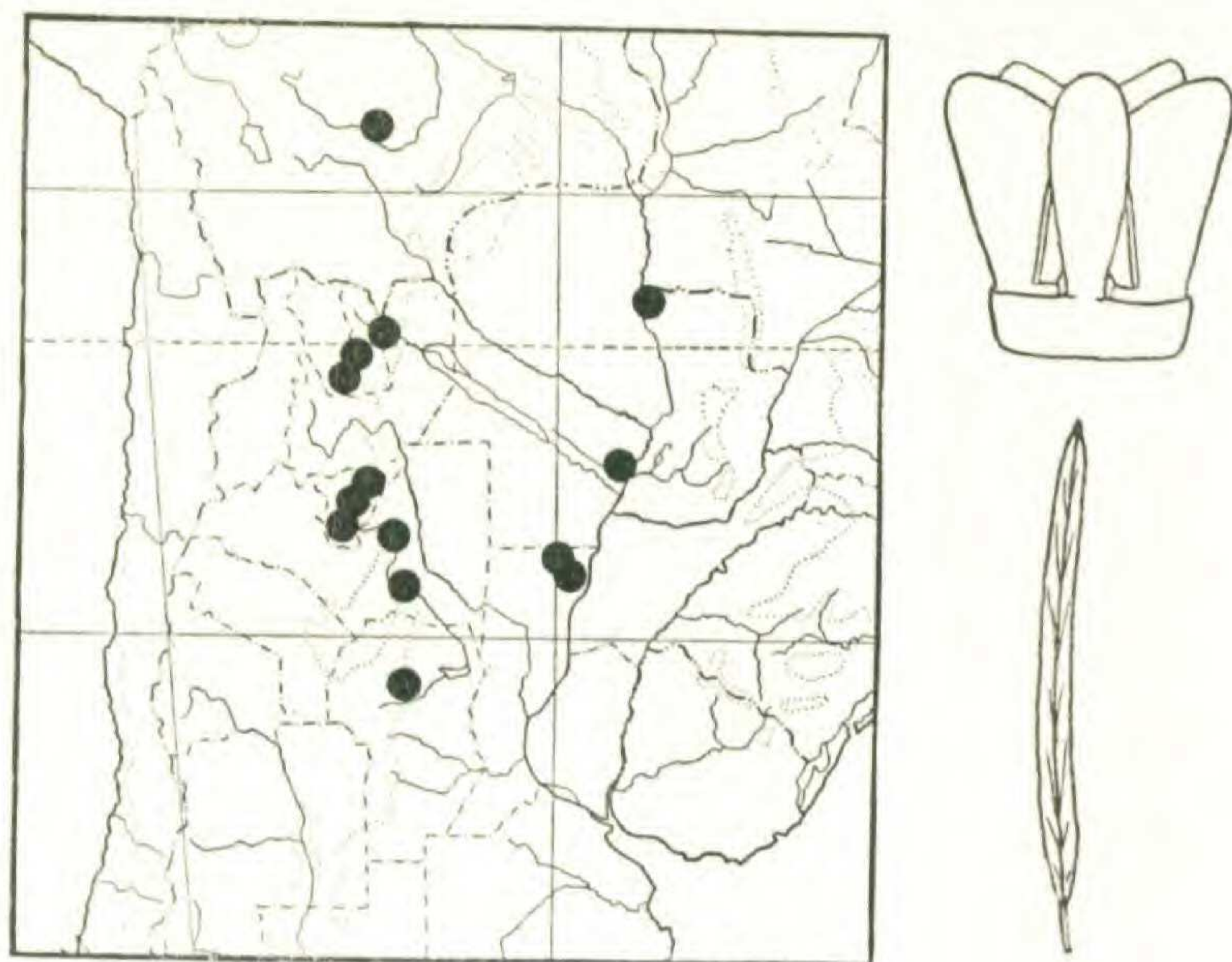


Fig. 10. Distribution, gynostegium, and leaf of *S. gracile*.

*Sarcostemma gracile* inhabits the llanos of northern Argentina and adjacent Bolivia and Paraguay. According to Meyer, it is halophytic, a fact which may account for its obvious reduction. It flowers from October to March.

BOLIVIA. SANTA CRUZ: Chilón, *Steinbach* 3964. CHACO: Curupenda, *Cárdenas* 2521; Tatarenda, *Fries* 1441.

PARAGUAY: Chaco Paraguayo, Puerto Casado, *Rojas* 2482; Santa Elisa, *Rojas* 2715; Pilcomayo River, *Morong* 1004, type of *S. carpophylloides* Morong.

ARGENTINA. CATAMARCA: Capital, *Castillón* 1065. CHACO: Fontana, *T. Meyer* 219. CÓRDOBA: Córdoba, *Kurtz* 4510, *Lassen* 86; Sierra Chica, *Kurtz* 207. FORMOSA: Formosa, *Jørgensen* 2599; Las Lomitas, *Parodi* 8436. JUJUY: San Pedro, *Venturi* 5318; Perico del Carmen, Estancia Peruco, *Venturi* s. n. LA RIOJA: Famatina, *Venturi* 7828; La Antigua, Pozo de la Orilla, *Castellanos* s. n. SALTA: Orán, Tartagal Villa, *Schreiter* 10844, 3573; 5 km. NW Embarcación, *West* 8443. SANTA FE: General Obligado, Los Amores, *Ragonese* 3115. SANTIAGO DEL ESTERO: La Banda, *Lillo* 6091; Recreo, *Stuckert* 23009; between Brea Pozo & Río Huayco Hondo, *Bartlett* 19753. TUCUMÁN: Burruyacu, El Timbo, *Venturi* 1718; Río Lules, *Lillo* 7860; Cruz Alta, Orillas Río Sali, *Venturi* 753; Campo Alegre, *Schreiter* 5915; Famailla, Bella Vista, *Venturi* 2730.

7. *SARCOSTEMMA CRISPUM* Benth. Pl. Hartw. 291. 1848. (T.: *Hartweg* s. n.).

*Sarcostemma heterophyllum* Engelm. ex Torr. Pac. R. R. Rept. 5 (App.): 362. 1857. (T.: *Wright* 1679!).

*Sarcostemma undulatum* Torr. in Bot. Mex. Bound. Surv. 161. 1859. (T.: *Parry* s. n.).

*Philibertia undulata* (Torr.) Gray, in Proc. Amer. Acad. 12:65. 1877.

*Philibertia linearis* (Decne.) A. Gray, var. *heterophylla* (Engelm. ex Torr.) Gray, Syn. Fl. 2<sup>1</sup>:88. 1878, as to basynym only.

*Philibertia crispa* (Benth.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:318. 1881.

*Philibertella crispa* (Benth.) Vail, in Bull. Torr. Bot. Club 24:307. 1897.

*Philibertella Hartwegii heterophylla* (Engelm. ex Torr.) Vail, loc. cit. 1897, as to basynym only.

*Philibertella heterophylla* (Engelm. ex Torr.) Cocker. in Bot. Gaz. 26:279. 1898, as to basynym only.

*Funastrum crispum* (Benth.) Schltr. in Fedde's Repert. 13:284. 1915.



- Funastrum lineare* (Decne.) Macbr. var. *heterophyllum* (Engelm. ex Torr.) Macbr. in Contr. Gray Herb. n. s. 49:50. 1917, as to basynym only.  
*Funastrum heterophyllum* (Engelm. ex Torr.) Standl. in Contr. U. S. Nat. Herb. 23:1170. 1924, as to basynym only.  
*Philibertia heterophylla* (Engelm. ex Torr.) Jepson, Man. Fl. Pl. Calif. 770. 1925, as to basynym only.  
*Sarcostemma lobata* Waterfall, in Rhodora 51:58. 1949. (T.: *Waterfall 7914 in Herb. Univ. Okla.*!).

Stems twining or trailing, green, glabrate to puberulent, the nodes densely white-pubescent; lateral branches few. Leaves narrowly to broadly lanceolate, acuminate, hastate, cordate or truncate, usually strikingly undulate-crispate, rarely not crispate, 3–10 cm. long, 0.5–3.0 cm. wide, subcoriaceous, puberulent above, the midrib usually white-pilose, without glands at the base, puberulent beneath, the midrib usually white-glabrous; petiole 0.4–0.8 cm. long. Inflorescences umbelliform, 4- to 7-flowered; peduncle 0.3–3.0 cm. long, glabrescent, much shorter than the subtending leaves; bracts linear, minute; pedicels 1.5–2.0 cm. long, glabrescent. Calyx lobes narrowly lanceolate, 3–6 mm. long, copiously puberulent on both surfaces; squamellae solitary, rarely paired. Corolla rotate-subcampanulate, greenish purple without, purple within, the tube 1 mm. long, the lobes ovate-elliptic, obtuse, 7–11 mm. long, puberulent without, glabrous within, ciliate. Gynostegium 3 mm. high, the column 1 mm. long. Anthers 1 mm. long, the apical appendage ovate, the pollinium-sacs oblongoid-cylindrical, 0.8 mm. long, with sagittate corpusculum; ring of the corona thin, revolute, scarcely adnate to the column; vesicles of the corona thin, revolute, scarcely adnate to the column; vesicles of the corona oblongoid-ovoid, constricted at their insertion upon the column, 1 mm. long. Ovaries 2 mm. long, glabrescent; stigma-head abruptly and shortly 2-apiculate. Follicles narrowly fusiform, long-attenuate, 8.5–12.3 cm. long, 1.3–1.9 cm. thick, puberulent, finely striate; seeds unequally biconvex, 7 mm. long, 3 mm. wide, obscurely rugose dorsally, minutely papillate ventrally; coma about 3 cm. long.

The crispate leaves and large, deep purple flowers combine to make this one of the most distinctive species in the genus. There is a poorly defined cline in the characters of the leaves: to the south and west the leaves generally are smaller, less crisped, and less pubescent on the midrib. I have seen specimens from Mexico which show no signs of crisping and have very narrowly lanceolate leaves. The ends of the cline are not sufficiently distinct for taxonomic recognition, however. I cannot conceive that this cline is the result of anything but a response to increasing aridity which leads to reduction of the lamina and consequent suppression of the marginal growth responsible for crispature. Since floral differences do not exist, hybridization probably does not play a role.

The rather confused synonymy of this species is explained in the discussion pertaining to *Sarcostemma cynanchoides* ssp. *Hartwegii*. *Sarcostemma crispum* seems nowhere to be common; Reverchon reports it to be local and rare around Dallas, Midland, and Austin, Texas, and other collectors indicate that it usually



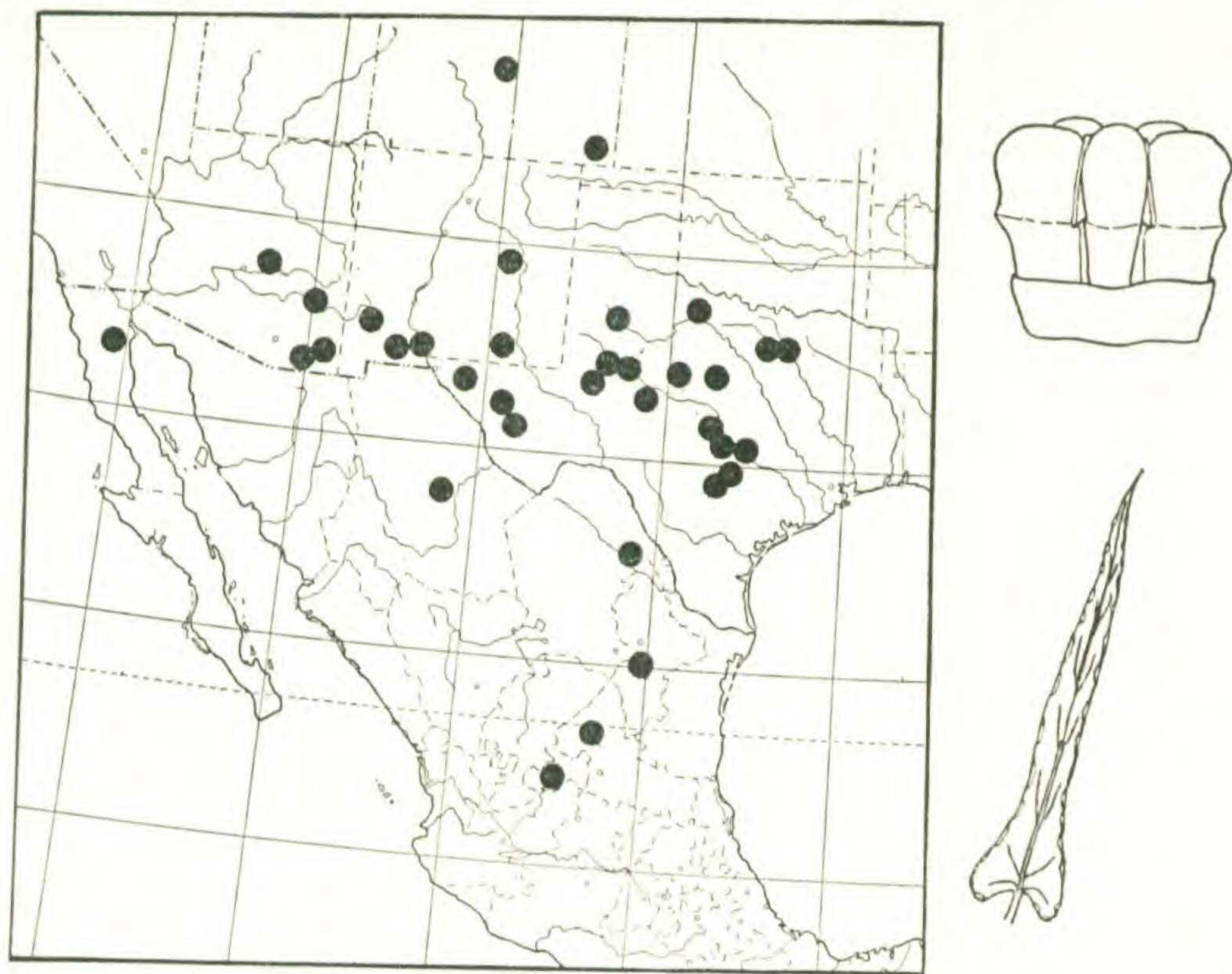


Fig. 11. Distribution, gynostegium, and leaf of *S. crispum*.

occurs scatteringly or in very small colonies. It grows at altitudes of 4000 to 7000 feet, chiefly in open, dry, rocky, or stony ground, and has been found in chaparral associated with *Zizyphus* and *Fallugia*. The blooming season ranges from May 9 to August 24. Fruiting specimens have been collected from May 13 to August 24. The distribution is from Colorado through Texas, New Mexico, and Arizona to central Mexico.

UNITED STATES. COLORADO: BACA CO.: S of Pritchett, *Harrington 3353*; FREMONT CO.: Phantom Canyon, *Christ 1090*. OKLAHOMA: CIMARRON CO.: N of Black Mesa, 3 mi. N of Kenton, *Waterfall 7914*, type of *S. lobata* Waterfall. TEXAS: BAYLOR CO.: Seymour, *Reverchon s. n.*; BEXAR CO.: San Antonio, *Schulz 793*; BLANCO CO.: *Wright 1678*; BREWSTER CO.: *Ferris & Duncan 2631*; CALLAHAN CO.: Baird, *E. J. Palmer 13688*; COMAL CO.: Fischer's Store, *E. J. Palmer 12209*; DALLAS CO.: Dallas, *Reverchon 601*; EASTLAND CO.: Eastland, *Oyster 2595*; GILLESPIE CO.: Grape Creek, *Jermy 134*; HOWARD CO.: Big Spring, *Eggert s. n.*; HUDSPETH CO.: Eagle Mts. near Hot Wells, *Waterfall 4964*; JEFF DAVIS CO.: Limpia, *Young 27*; LLANO CO.: *Bray 336½*; LUBBOCK CO.: Lubbock, *Reed 3694*; MIDLAND CO.: Midland, *Tracy 7980*; MITCHELL CO.: Colorado, *Eggert s. n.*; TARRANT CO.: *Ruth 740*; TAYLOR CO.: Abilene, *Tracy 7979*; TOM GREEN CO.: Dove Creek, *Tweedy 235*; TRAVIS CO.: Austin, *E. Hall 518*. NEW MEXICO: DONA ANA CO.: Organ Mts., *Wooton s. n.*; EDDY CO.: Queen, *Wooton s. n.*; GRANT CO.: Central, *Mulford 406*; GUADALUPE CO.: Santa Rosa, *Arsène 19470*; LUNA CO.: Deming, *Goldman 1445*. ARIZONA: COCHISE CO.: Rhoda Rigg's Ranch, Chiricahua Mts., *Blumer 1499*; GILA CO.: Collom Camp, Matzatzal Mts., *Collom 575*; GRAHAM CO.: 10 mi. above Clifton, *Hough s. n.*

MEXICO. BAJA CALIFORNIA NORTE: near Ciénaga, S end of Sierra Juárez, *Wiggins 9148*. CHIHUAHUA: near Chihuahua, *Pringle s. n.*, 546, 1326; W from Pearson, *Barlow s. n.*; Sta. Eulalia Plains, *Wilkinson s. n.* COAHUILA: 5 km. NE Sta. Elena, *R. M. Stewart 605*; 2-3 km. N Puerto Colorado, *I. M. Johnston 8681*; San Lázaro, *Wynd & Muller 101*. NUEVO LEON: 15 miles SW Galeana, *Muller & Muller 1084*. SAN LUIS POTOSÍ: Charcas, *Lundell 5074*.



8. *SARCOSTEMMA ELEGANS* Decne. in DC. Prodr. 8:541. 1844. (T.: *Berlandier 602 in Herb. Paris!*).

*Sarcostemma bicolor* Decne. loc. cit. 1844. (T.: *Galeotti 1537 in Herb. Paris!*).

*Sarcostemma luridum* Kunze, in Linnaea 20:26. 1847, ex char. (T.: *Schleiden s. n.*).

*Philibertia elegans* (Decne.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:318. 1881.

*Philibertia lurida* (Kze.) Hemsl. loc. cit. 319. 1881.

*Philibertia bicolor* (Decne.) Gray, in Proc. Amer. Acad. 21:395. 1886.

*Philibertella elegans* (Decne.) Vail, in Bull. Torr. Bot. Club 24:310. 1897.

*Funastrum elegans* (Decne.) Schltr. in Fedde's Repert. 13:284. 1915.

*Funastrum luridum* (Kze.) Schltr. loc. cit. 286. 1915.

*Funastrum bicolor* (Decne.) Macbr. in Contr. Gray Herb. n. s. 49:50. 1917.

*Funastrum bicolor* (Decne.) Standl. in Contr. U. S. Nat. Herb. 23:1172. 1924.

Stems twining or trailing, gray-green, glabrescent to copiously pilosulose; lateral branches few. Leaves broadly lanceolate to oblong, acute to mucronate, deeply cordate, the lobes descending, 2–5 cm. long, 1.0–4.5 cm. wide, subcoriaceous, glabrescent to copiously puberulent on both surfaces, with one or more glands on the midrib at the base; petiole 0.6–2.2 cm. long. Inflorescences umbelliform, 4- to 7-flowered; peduncle 0.5–1.8 cm. long, minutely puberulent, much shorter than the subtending leaves; bracts linear, 0.1–0.2 cm. long; pedicels 1.0–2.5 cm. long, puberulent. Calyx lobes ovate, 4–6 mm. long, densely puberulent without, puberulent within; squamellae alternate, usually solitary. Corolla rotate-subcampanulate, yellow, with a deep purple spot at the base of each lobe, often extending upward as a median streak, or entirely suffused with purple on the inner surface, greenish without, the tube 3.5 mm. long, the lobes ovate-lanceolate, obtuse, 9–13 mm. long, minutely puberulent without, glabrescent within. Gynostegium 3.5 mm. high, the column about 1 mm. long. Anthers 1.5 mm. long, the apical appendage suborbicular, the pollinium-sacs oblongoid-cylindrical, 0.7 mm. long, with sagittate corpusculum; ring of the corona thin, adnate to the base of the corona vesicles; vesicles of the corona oblongoid to subspheroid, the inner side often apiculate at the tip, or with a vertical keel, 2.5 mm. long. Ovaries 2.5 mm. long, glabrous; stigma-head conical, with 2 long apiculae. Follicles narrowly fusiform-obclavate, 7.6 cm. long, 1.2 cm. thick, minutely puberulent, finely striate; seeds unequally biconvex, 7 mm. long, 3 mm. wide, obscurely rugose on both surfaces; coma about 3 cm. long.

*Sarcostemma elegans* is closest, morphologically, to *S. Torreyi*, from which it differs in the short peduncles, relatively short leaves, and the long, apiculate stigma-head. *S. elegans* occurs in the Central Plateau region of Mexico, while *S. Torreyi* is found in the northern desert areas of Mexico and adjacent Texas. As indicated in the key, the two species form a close-knit group more or less isolated from the other species in the section. Probably they have either differentiated from a common ancestor occupying the area from central Mexico to Texas, or the southern species may have migrated to the north giving rise to *S. Torreyi* in this changed habitat. The floral differences between the species are such that hybridization would appear to be difficult, e. g. the length of the column and stigma-head



appendages in *S. elegans* would result in the pollinia being affixed to different insects or to different places upon the same species of insect. There is a narrow gap in the ranges; however, there are several specimens (*Stanford, Retherford & Northcraft 869, Reko 5259*) which I interpret as hybrids between *S. elegans* and *S. Torreyi*. Apparently these are back-crosses, for they are sufficiently close to one or the other of the putative parents to be easily referred to either species. The precise effects of this hybridization cannot be determined without the use of population studies. The most satisfactory way of handling such a problem taxonomically appears to be to refer the hybrids to whichever species they are morphologically and geographically closest. Unfortunately, this has the disadvantage of obscuring the interesting genetic implications. *Funastrum vesiculare* apparently is a hybrid which is very close to *S. Torreyi*, from which it differs, however, in the direction of *S. elegans*; I have referred it to the former species.

*Sarcostemma elegans* has been found growing chiefly on rocky slopes or lava fields at altitudes from 5000 to 8000 feet. Flowering specimens are dated from January 1 to October 27; the single fruiting specimen is dated August 2.

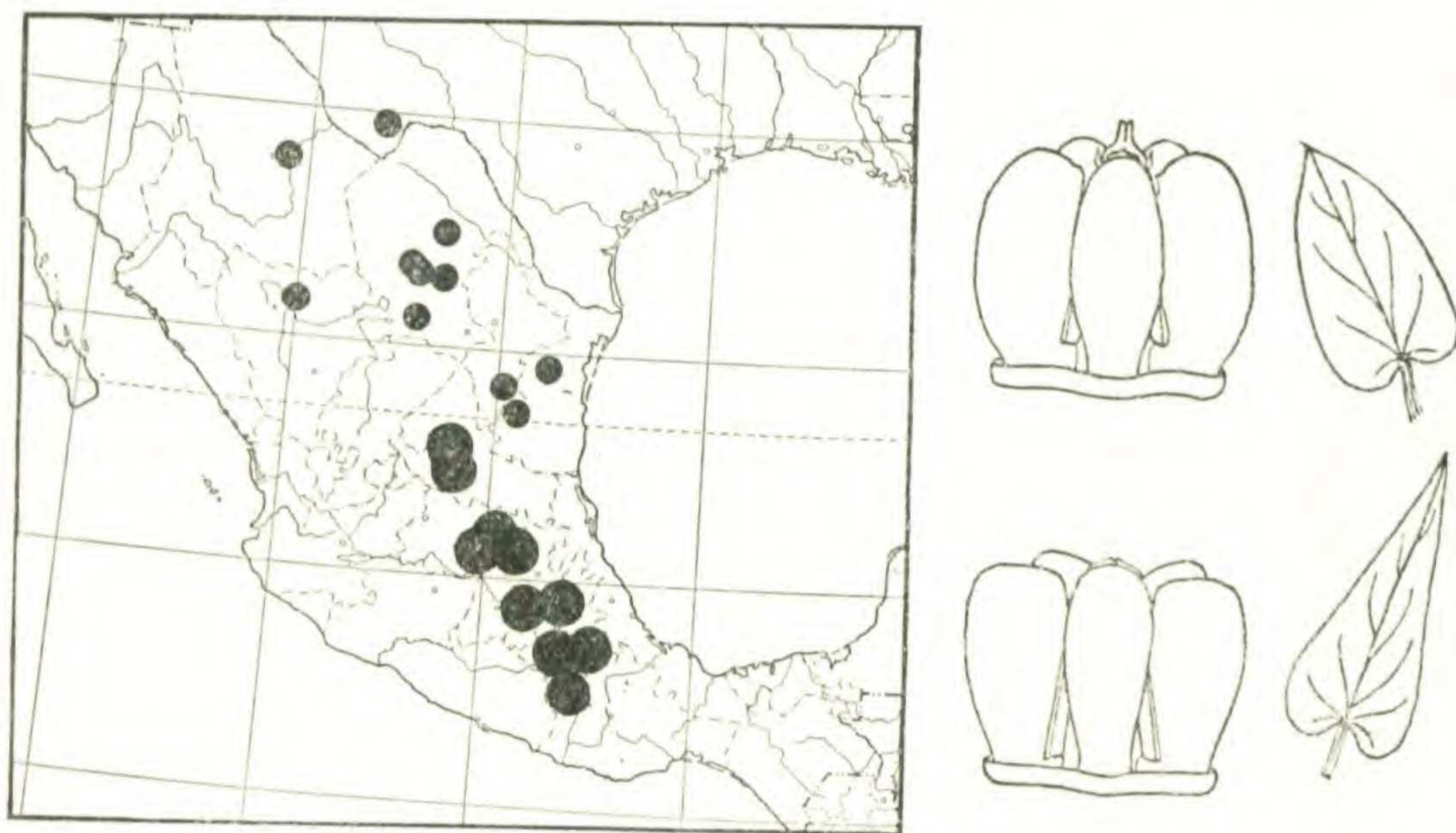


Fig. 12. Gynostegium and leaf of *S. elegans* (upper row), of *S. Torreyi* (lower row). Distribution of *S. elegans* (large dots), of *S. Torreyi* (small dots).

MEXICO. DISTRITO FEDERÁL: Pedregál, *Lyonnet 29*; San Gerónimo, *Russell & Souviron 127*; near Mexico City, *Berlandier 602*, type of *S. elegans* Decne. GUANAJUATO: Guanajuato, *Duges 101*. HIDALGO: Ixmiquilpan, *Purpus 1379*; *Rose, Painter & Rose 8943*. JALISCO: near Zapotlán, *Pringle 5496*. MÉXICO: Temascaltepec, *Socobon, Hinton 7225*; Crucero Agua Blanca, *Hinton 4936*; Valley of México, near San Angel, *Rose, Painter & Rose 9499*; near Tlalpam, *Rose, Painter & Rose 8250, Pringle 13116, Rose & Hough 4529*; Santa Fe, *Bourgeau 318*. MICHOACÁN: Coalcomán, Barroloso, *Hinton 15075*. OAXACA: Nochixtlan, barrancas de Puebla Viejo, *Conzatti 1842*; Tenango, *L. C. Smith 390*. PUEBLA: near San Luis Tultitlanapa, *Purpus 3241*; near Tehuacán, *Pringle 6760, Mohr s. n., Rose, Painter & Rose 9953, Galeotti 1537*, type of *S. bicolor* Decne.; El Riego, *Purpus 1258*; Rancho Posado, *Nicolas 47*. QUERETARO: near San Juan del Río, *Rose, Painter & Rose*



9669, *Altamirano* 1973. SAN LUIS POTOSÍ: Bocas, *Pringle* 3564; Silos, *Purpus* 482; near San Luis Potosí, *Parry & Palmer* 589, *Schaffner* 316; mts. near San Miquelito, *Schaffner* 649. TLAXCALA: Tlaxcala, *Balls* 4908. VERA CRUZ: Orizaba, *Botteri* 979.

9. SARCOSTEMMA TORREYI (Gray) Woods. in *Ann. Mo. Bot. Gard.* 28:217. 1941.

*Philibertia Torreyi* A. Gray, in *Proc. Amer. Acad.* 12:64. 1877. (T.: *Parry* s. n.).

*Philibertia Torreyi* (Gray) Vail, in *Bull. Torr. Bot. Club* 24:309. 1897.

*Funastrum Torreyi* (Gray) Schltr. in *Fedde's Repert.* 13:287. 1915.

*Funastrum vesiculare* Woods. in *Amer. Jour. Bot.* 22:687. 1935. (T.: *Bartlett* 10318 in *Herb. Univ. Mich.*!).

Stems twining or trailing, gray or green, pilosulose; lateral branches few. Leaves lanceolate, acuminate to acute, cordate, the lobes descending, 1.5–4.0 cm. long, 1.0–2.5 cm. wide, subcoriaceous, pilosulose on both surfaces with one or more glands on the midrib at the base; petiole 0.7–1.4 cm. long. Inflorescences umbelliform, 7- to 10-flowered; peduncle 1.0–3.5 cm. long, pilosulose; bracts linear, 0.1–0.2 cm. long; pedicels 0.8–1.6 cm. long, pilosulose. Calyx lobes ovate-lanceolate, 4–6 mm. long, puberulent on both surfaces; squamellae solitary, rarely paired. Corolla rotate-subcampanulate, cream-colored with a purple spot at the base and a median purple spot on each lobe, lobes ovate, acute, 7–11 mm. long, minutely puberulent without, glabrate within, scarious-ciliate. Gynostegium 3 mm. high, the column very short. Anthers 1.5 mm. long, the apical appendage suborbicular to subreniform, the pollinium-sacs oblongoid-cylindrical, 0.8 mm. long, with sagittate corpusculum; ring of the corona fleshy, adnate to the base of the corona vesicles; vesicles of the corona oblongoid to obovoid, 2.5 mm. long. Ovaries 2.5 mm. long, glabrous; stigma-head subconical, obscurely bilobed. Follicles fusiform, long-attenuate, 8.2 cm. long, 1.2 cm. thick, finely striate; seeds somewhat flattened, 7 mm. long, 4 mm. wide, minutely papillate on both surfaces; coma about 3 cm. long.

A relatively rare and local species, the relations of which to *S. elegans* are discussed in connection with the latter. *Sarcostemma Torreyi* inhabits dry hillsides and scrubby woodland associations in northern Mexico and southwestern Texas. It has been collected at altitudes of 4500 to 7200 feet. Judging by the relatively few specimens, it flowers from May 29 to August 18; fruits have been collected in July and September.

UNITED STATES. TEXAS: BREWSTER CO.: Chisos Mts., *Sperry* 481; PRESIDIO CO.: Fresno Canyon, N of Lajitas, *Cutler* 1893.

MEXICO. CHIHUAHUA: Sta. Eulalia Mts., *Pringle* 63, 550, 1325. COAHUILA: Muzquiz, slopes of Sierra de San Manuel, *Wynd & Muller* 331; Parras, *Purpus* 4679, *Stanford*, *Retherford & Northcraft* 164; Cuatro Ciénegas, Sierra de la Madera, *Muller* 3168; Sierra de la Gloria, SE Monclova, *Marsh* 1915; Sierra de Sta. Rosa, S of Muzquiz, *Marsh* 1413. DURANGO: Inde, *Reko* 5259. NUEVO LEON: Dulces Nombres, *Meyer & Rogers* s. n.; Monterrey, *Muller* 248. TAMAULIPAS: Cerro Tinaja, near San José, *Bartlett* 10318, type of *F. vesiculare* Woods.; 22 km. SE of Miquihuana, *Stanford*, *Retherford & Northcraft* 869.



10. *SARCOSTEMMA CYNANCHOIDES* Decne. in DC. Prodr. 8:540. 1844.

## KEY TO THE SUBSPECIES

- a. Leaves broadly lanceolate, 3–4 times as long as broad, cordate (rarely truncate) at the base; flowers white, the corona vesicles widest above the middle..... 10a. *S. cynanchoides*  
ssp. *cynanchoides*
- aa. Leaves narrowly lanceolate, more than 3–4 times as long as broad, hastate (rarely truncate or obtuse); flowers purple or pink, or the corolla lobes with a median purple streak, the corona vesicles widest below the middle..... 10b. *S. cynanchoides*  
ssp. *Hartwegii*

10a. *SARCOSTEMMA CYNANCHOIDES* Decne. ssp. ***cynanchoides*** (Decne.) R. Holm, stat. nov.

*Sarcostemma cynanchoides* Decne. in DC. Prodr. 8:540. 1844. (T.: *Berlandier 2324 in Herb. Paris!*).

*Philibertia cynanchoides* (Decne.) Gray, in Proc. Amer. Acad. 12:64. 1877.

*Philibertia cynanchoides* var. *subtruncatum* Robins. & Fern. in Proc. Amer. Acad. 30:119. 1894. (T.: *Hartmann 4 in Herb. U. S. Nat. Mus.!*).

*Philibertella cynanchoides* (Decne.) Vail, in Bull. Torr. Bot. Club 24:307. 1897.

*Funastrum cynanchoides* (Decne.) Schltr. in Fedde's Repert. 13:284. 1915.

*Funastrum cynanchoides* var. *subtruncatum* (Robins. & Fern.) Macbr. in Contr. Gray Herb. n. s. 49:51. 1917.

Stems twining or trailing, green to gray-green, glabrous to sparsely puberulent; lateral branches many. Leaves broadly ovate-lanceolate, acuminate to acute, cordate, rarely truncate or somewhat hastate, the lobes usually diverging, 2–3 cm. long, 0.5–3.0 cm. wide, membranaceous, sparsely puberulent on both surfaces, with one or more glands on the midrib at the base; petiole 0.9–1.5 cm. long. Inflorescences umbelliform, 12- to 20-flowered; peduncle 3.5–4.0 cm. long, glabrescent; bracts linear, minute; pedicels slender, 1.5–1.7 cm. long, minutely pilosulose. Calyx lobes ovate, 2–3 mm. long, pilosulose without, glabrous within; squamellae absent, solitary, or paired. Corolla rotate-subcampanulate, greenish-white, rarely pinkish, the tube 2 mm. long, the lobes ovate, acute, 6–7 mm. long, glabrescent without, glabrous within, more or less ciliolate. Gynostegium 2 mm. high, the column about 0.5 mm. long. Anthers 1 mm. long, the apical appendage suborbicular, the pollinium-sacs oblongoid-cylindrical, 0.6 mm. long, with sagittate corpusculum; ring of the corona thin, revolute, not adnate to the base of the corona vesicles; vesicles of the corona suboblongoid, widest above the middle, 1.5 mm. long. Ovaries 1.5 mm. long, glabrous; stigma-head convex, obscurely bilobed. Follicles fusiform, 6.5–7.2 cm. long, 1.0–1.3 cm. thick, puberulent, finely striate; seeds unequally biconvex, 7–8 mm. long, 3–4 mm. wide, minutely papillate on both surfaces, the margin serrate; coma about 3.5 cm. long.

As interpreted here, *Sarcostemma c. cynanchoides* represents the eastern subspecies of a species ranging from Oklahoma and central Texas to western Mexico and California. While it usually can be distinguished easily from the western subspecies by its broader, shorter leaves and white flowers, these differences do not appear to be sufficiently important for specific designation. *Sarcostemma c. cynan-*



*chooides* occupies less arid habitats and shows less evidence of morphological reduction than its western relative. It also begins to flower nearly two months later. Floral differentiation between the two subspecies is not striking: *S. c. cynanchoides* has a somewhat longer column and the corona vesicles are widest above the middle in the majority of specimens. Hybridization between them appears to be rather rare (time of flowering may be a barrier), but the area of overlap of the two ranges is in Mexico where few specimens have been collected. The nature of the cline is further discussed in connection with *Sarcostemma c. Hartwegii* (10b).

*Sarcostemma c. cynanchoides* has been found climbing trees and shrubs in the sandy soil of rivers and ditches and in rocky canyons; it grows at altitudes of 1600 to 6400 feet. Blooming dates range from May to September and fruit have been collected in August and September.

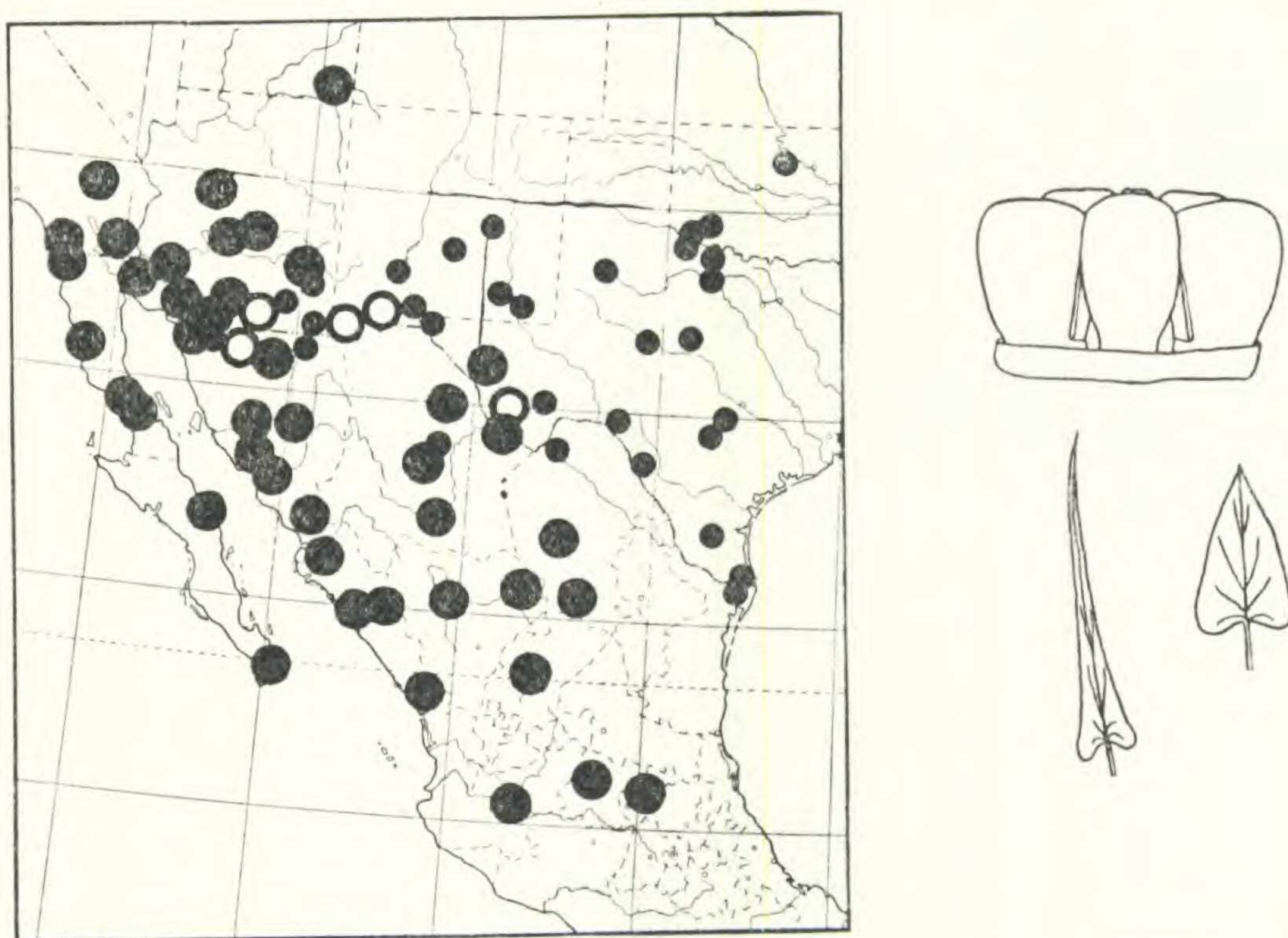


Fig. 13. Distribution of *S. cynanchoides cynanchoides* (small dots), of *S. cynanchoides Hartwegii* (large dots), of putative hybrids (black circles). Gynostegium of *S. cynanchoides* spp. (upper right); leaf of *S. cynanchoides Hartwegii* (lower left), of *S. cynanchoides cynanchoides* (lower right).

UNITED STATES. OKLAHOMA: COMANCHE CO.: Fort Sill, *Clemens* 11734; PAYNE CO.: Ripley, *Stratton* 237; TELLMAN CO.: S of Davidson, *Goodman* 2266. TEXAS: ARCHER CO.: Kickapoo Creek, *Reverchon* 602; BEXAR CO.: San Antonio, *Wilkinson* s. n.; BREWSTER CO.: Chisos Mts., *Tharp* 3650; BROWN CO.: Jim Ned Creek, *Reverchon* s. n.; CAMERON CO.: Brownsville, *Schulz* 2094; COMAL CO.: New Braunfels, *Lindheimer* 993; DUVAL CO.: Pena, *Nealley* 375; EL PASO CO.: El Paso, *Stearns* 125; HALL CO.: Estelline, *Reverchon* 3875; LUBBOCK CO.: Slaton, *Reed* 3228; MAVERICK CO.: Eagle Pass, *Havard* s. n.; TOM GREEN CO.: Soular d s. n.; VALVERDE CO.: Devil's River, *Eggert* s. n.; WILBARGER CO.: Vernon, *Ferris & Duncan* 3352; YOUNG CO.: Graham, *Reverchon* 3199. NEW MEXICO: CHAVES CO.: Roswell, *Earle & Earle* 242; DONA ANA CO.: Mt. Selden, *Rusby* 261; EDDY CO.: Dark Cañon, 45 miles SW of Carlsbad, *Grassl* 98; GUADALUPE CO.: Sta. Rosa, *Arsène & Benedict* 16950; LINCOLN CO.: above Tularosa, *Wootton & Standley* s. n.; LUNA CO.: Florida Mts., *Mulford* 1041a; SIERRA CO.: Animas Creek, *Metcalf* 1128. ARIZONA: COCHISE CO.: Bisbee, *Mearns* 879; GRAHAM CO.: Clifton, *Hough* s. n.; PIMA CO.: Tucson, *Kearney & Peebles* 14989.



MEXICO. CHIHUAHUA: Rio Carmen, N of Chihuahua, *Wislizenus* 105; Paso del Norte, *Pringle* 1324; Sta. Eulalia Plains, *Wilkinson* s. n. COAHUILA: Matamoros, *Berlandier* 2324, type of *S. cynanchoides* Decne., 904, 2334; Del Carmen Mts., *Marsh* 840. NUEVO LEON: El Carrizo, *Pringle* 13117; Río Brazo del Norte, *Schott* s. n. SONORA: Fronteras, *Hartmann* 4, type of *P. c.* var. *subtruncatum* Robins. & Fern., 984, 985; Guadalupe Canyon, *Merton* 2053.

10b. *SARCOSTEMMA CYNANCHOIDES* Decne. ssp. **Hartwegii** (Vail) R. Holm, stat. nov.

*Sarcostemma lineare* Decne. ex Benth. Pl. Hartw. 25. 1840, non Sprengel. (T.: *Hartweg* 217!).

*Sarcostemma heterophyllum* Engelm. sensu Torr. in Bot. Mex. Bound. Surv. 162. 1859, as to specimens cited, not as to type.

*Philibertia linearis* (Decne.) Gray, Proc. Amer. Acad. 12:64. 1877.

*Philibertia linearis* var. *heterophylla* (Engelm. sensu Torr.) Gray, Syn. Fl. 2<sup>1</sup>:88. 1878, as to description, not as to type.

*Philibertella Hartwegii* Vail, in Bull. Torr. Bot. Club 24:308. 1897, based on *S. lineare* Decne.

*Philibertella Hartwegii heterophylla* (Engelm. sensu Torr.) Vail, loc. cit. 1897, as to specimens cited, not as to type.

*Philibertella heterophylla* (Engelm. sensu Torr.) Cocker. in Bot. Gaz. 26:279. 1898, based on *P. Hartwegii heterophylla* (Engelm. sensu Torr.) Vail.

*Funastrum Hartwegii* (Vail) Schltr. in Fedde's Repert. 13:285. 1914.

*Funastrum lineare* (Decne.) Macbr. in Contr. Gray Herb. n. s. 49:50. 1917.

*Funastrum lineare* var. *heterophyllum* (Engelm. sensu Torr.) Macbr. loc. cit. 1917, based on *P. Hartwegii heterophylla* (Engelm. sensu Torr.) Vail.

*Funastrum heterophyllum* (Engelm. sensu Torr.) Standl. in Contr. U. S. Nat. Herb. 23:1170. 1924, as to description, not as to type.

*Philibertia heterophylla* (Engelm. sensu Torr.) Jepson, Man. Fl. Pl. Calif. 770. 1925, as to description, not as to type.

Stems twining or trailing, green, glabrate to puberulent, the nodes white puberulent; lateral branches many. Leaves narrowly lanceolate, acuminate, hastate, or cordate, sometimes obtuse, the lobes diverging, 1–11 cm. long, 0.1–2.5 cm. wide, membranaceous, glabrate to subpuberulent on both surfaces, with one or more glands on the midrib at the base; petiole 0.9–1.9 cm. long. Inflorescences umbelliform, 7- to 14-flowered; peduncle slender, 0.5–5.5 cm. long, pilosulose; bracts linear, minute; pedicels slender, 0.7–1.5 cm. long, puberulent. Calyx lobes ovate-linear, 2–3 mm. long, pilosulose without, glabrous within; squamellae usually solitary. Corolla rotate-subcampanulate, purple to pink, or the lobes each with a median purple streak, the tube 1 mm. long, the lobes ovate, acuminate to acute, 5–7 mm. long, puberulent without, glabrous within, ciliate. Gynostegium 2.5 mm. high, the column very short. Anthers 1 mm. long, the apical appendage suborbicular, the pollinium-sacs oblongoid-cylindrical, with ellipsoid-sagittate corpusculum; ring of the corona prominent, not adnate to the base of the corona vesicles; vesicles of the corona rectanguloid, widest below the middle, 1.5 mm. long. Ovaries 1.5 mm. long, glabrous; stigma-head convex, obscurely bilobed. Follicles slender, fusiform, attenuate, 7.4–11.0 cm. long, 0.6–1.0 cm. thick, minutely puberulent, finely striate; seeds unequally biconvex, 6 mm. long, 1.5 mm. wide, minutely rugose dorsally, minutely papillate ventrally; coma about 3.5 cm. long.



The taxonomy of this subspecies and of *S. crispum* is confused by the widespread misapplication of the name *S. heterophyllum* Torr. In 1859, Torrey published this manuscript name of Engelmann, citing but one specimen, *Wright 1679*, which must be regarded as the type. This specimen, however, is an example of *S. crispum* with very narrow leaves in which crisping or undulation is not apparent. Two years later, Torrey referred *Wright 1681* of the Mexican Boundary Survey collections to *S. heterophyllum*. This specimen proves to be *S. cynanchoides Hartwegii* and the description given by Torrey clearly applies to that subspecies. All later authors have followed this misapplication of the name in making various combinations in *Philibertia*, *Philibertella*, and *Funastrum*.

Inasmuch as the type of the first-published *S. heterophyllum* actually is *S. crispum*, this name and subsequent combinations are nomenclaturally related to *S. crispum* and unavailable for the lanceolate-leaved subspecies of *S. cynanchoides*. The epithet *lineare* also is pre-empted by the earlier name of Sprengel. I have preferred to employ *Hartwegii*, rather than coin a new name, despite the fact that, owing to this early misunderstanding, it never was used widely.

*Sarcostemma c. Hartwegii* is similar to the eastern subspecies in most respects, differing in the narrower, longer leaves and purple flowers. Intergradation between the two forms appears to be uncommon, but occurs in a narrow northwest-southeast belt from Arizona to central Mexico. Hybridization has produced an abruptly stepped cline and intermediate forms have been designated as *S. c. cl. cynanchoides-Hartwegii*.

In contradistinction to *S. c. cynanchoides*, *S. c. Hartwegii* usually grows in dry, sandy or rocky soil of arroyos and plains. Occasionally it is found in cultivated bottom lands and ditches, in which case the flowers are larger and the leaves often fully ten times as large as normal. The altitudinal range is from 100 to 5000 feet, overlapping that of the eastern subspecies. Flowering specimens have been collected from February to early September, this season beginning about two months before that of *S. c. cynanchoides*. Fruiting specimens dated from April to October have been seen.

UNITED STATES. UTAH: SAN JUAN CO.: 6 miles above mouth of San Juan River, *Cutler 3180*; Forbidding Canyon, near Colorado River, *Cutler 2831*. TEXAS: BREWSTER CO.: Chisos Mts., *Muller 8117*; CULBERSON CO.: near Van Horn, *Waterfall 5447*; PRESIDIO CO.: Presidio, *Havard s. n.* NEW MEXICO: DONA ANA CO.: mesa W of Organ Mts., *Standley s. n.*; LUNA CO.: Florida Mts., *Mulford 1063*. ARIZONA: GILA CO.: Collom Camp, Matzatzal Mts., *Collom 6*; GRAHAM CO.: near Safford, *Maguire 10931*; PIMA CO.: near Sta. Rosa, *Cutler 4724*; PINAL CO.: near Mammoth, *Peebles 14611*; MARICOPA CO.: 23 miles N of Phoenix, *Gillespie 8660*; YAVAPAI CO.: near Congress Junction, *Gillespie 8502*. CALIFORNIA: IMPERIAL CO.: near Ogilby, *Alexander & Kellogg 1951*; LOS ANGELES CO.: Covina, *G. B. Grant 972*; RIVERSIDE CO.: Snow Creek Canyon, San Jacinto Mts., *Munz 12397*; SAN BERNARDINO CO.: San Bernardino Valley, *Parish & Parish 309*; SAN DIEGO CO.: Box Canyon, *Munz & Hitchcock 12048*.

MEXICO. BAJA CALIFORNIA NORTE: Punta Prieta, *Wiggins 7738*; 30 miles N of Punta Prieta, *Wiggins 5346*; San Quintín Bay, *E. Palmer 639*; 14.5 miles E of Agua Caliente, *Keck 1925*. BAJA CALIFORNIA SUR: Mulege, *Johnston 3684*; Santa Agueda, *E. Palmer 231*; near San José del Cabo, *Wiggins 5682*. CHIHUAHUA: Bachimba, S of Chihuahua, *Wislizenus 255*; near Chihuahua, *E. Palmer 84*, *Pringle 1051*; Sta. Eulalia Plains, *Wilkinson*



*s. n.*; 5 miles E of Allende turn-off, road Parral-Camargo, Freytag & Baxter 65. COAHUILA: Movans, Purpus 4485; 10 miles N of Cuatro Ciénegas, Wynd 738; near Parras, Shreve 8761; Torreon, Pittier 505. DURANGO: Santiago Papaquiario, Nelson 4661, E. Palmer 39. GUANAJUATO: Guanajuato, Duges 7. JALISCO: near Guadalajara, Pringle 5885, 8497, 11628, Safford 1426. QUERÉTARO: near San Pablo, Rose, Painter & Rose 9817; between Huiguerilla and San Pablo, Altamirano 7702. SINALOA: San Blas, M. E. Jones 23249; Villa Union, Lamb 445; Altata, Rose 1375; Culiacán, Partidas 2015, 2016; San Ignacio, Montes & Salazar 53; near Fuerte, Rose, Standley & Russell 13928; near Villa Union, Rose, Standley & Russell 14639. SONORA: Cocorit, Yaqui Valley, Gentry 888; San Bernardo, Río Mayo, Gentry 1308; 5.7 miles NW of Caborca, Wiggins 8265; near Suhuoral, Wiggins & Rollins 264; 24 miles SW of Sonoyta, Shreve 7588; 35.3 miles SW of Sonoyta, Wiggins 8363; near Guaymas, San Carlos Bay, Ferris 8730; Rancho San Ignacio, 10 miles N of Vicam, Wiggins 6461; Forin, Studhalter 1370; near Cucurpe, Wiggins 7170; Hermosillo, Maltby 198; Alamos, Goldman 307; Pitequito, Kennedy 7080, Keck 4014; near Altar, Long 10; near Magdalena, Rose, Standley & Russell 15065; Realito, 10 miles E of Altar, Shreve 6371; Navajoa, Rose, Standley & Russell 13134; 20 miles N of Sargento, Mallery & Turnage *s. n.* ZACATECAS: Cedros, Lloyd 123.

SARCOSTEMMA CYNANCHOIDES cl. CYNANCHOIDES-HARTWEGII.

UNITED STATES. TEXAS: PRESIDIO CO.: 24 miles S of Marfa, Hinchley 1051. NEW MEXICO: HIDALGO CO.: Virdin, Hershey A-11; LUNA CO.: Florida Mts., Mulford 1041a. ARIZONA: PIMA CO.: Rincon Mts., Harrison & Kearney 5820.

MEX.CO. SONORA: along Río de los Alisos, 31 miles S of Nogales, Wiggins 7034A.

11. *SARCOSTEMMA hirtellum* (A. Gray) R. Holm, comb. nov.

*Sarcostemma heterophyllum* Engelm. sensu Torr. var. *hirtellum* Gray, in Brewer & Watson, Bot. Calif. 1:178. 1876. (T.: Cooper *s. n.*!).

*Philibertia linearis* (Decne.) Gray, var. *hirtella* Gray, Syn. Fl. 2<sup>1</sup>:88. 1878.

*Philibertia hirtella* (Gray) Vail, in Bull. Torr. Bot. Club 24:309. 1897.

*Philibertia hirtella* (Gray) Parish, in Muhlenbergia 3:126. 1907.

*Funastrum hirtellum* (Gray) Schltr. in Fedde's Repert. 13:286. 1915.

Stems twining, trailing, or semi-erect, gray-green, densely canescent; lateral branches many. Leaves linear to narrowly lanceolate, acuminate to acute, obtuse, rarely truncate, 1.0–3.6 cm. long, 0.1–0.5 cm. wide, pilosulose on both surfaces, coriaceous, without glands on the midrib; petiole 0.1–1.5 cm. long. Inflorescences umbelliform, 9- to 12-flowered; peduncle 1.5–4.9 cm. long, pilosulose; bracts linear, minute; pedicels 0.6–0.9 cm. long, pilosulose. Calyx lobes linear, 2.0–2.5 mm. long, densely subpilose on both surfaces; squamellae absent or solitary. Corolla rotate-subcampanulate, white, the tube 1 mm. long, the lobes ovate-lanceolate, acute, 4–5 mm. long, glabrous without, subpilose within, ciliolate. Gynostegium 2 mm. high, the column about 0.5 mm. long. Anthers 0.75 mm. long, the apical appendage ovate-elliptic, the pollinium-sacs somewhat flattened, 0.5 mm. long, with ellipsoid to narrowly sagittate corpusculum; ring of the corona thin, adnate to the base of the corona vesicles; vesicles of the corona oblongoid, 1.5 mm. long. Ovaries 1.5 mm. long, essentially glabrous; stigma-head slightly convex, obscurely bilobed. Follicles paired, narrowly fusiform, grayish-yellow, waxy, 3.8–4.7 cm. long, 0.3–0.5 cm. thick, very minutely but thickly puberulent; seeds somewhat flattened, 8 mm. long, 4 mm. wide, rugose-papillate dorsally, minutely papillate ventrally; coma about 2.5 cm. long.



*Sarcostemma birtellum* has a restricted distribution in the Colorado and Mojave deserts in Nevada, California, and Arizona. It has been confused in the herbarium with *S. cynanchoides Hartwegii* from which it differs in the narrow, pubescent leaves, canescent aspect, and semi-erect habit, in addition to important, though less prominent, floral differences. In contradistinction to all other species in the New World, *S. birtellum* appears invariably to have paired follicles which diverge markedly from one another. The species probably is most closely related to the western subspecies of *S. cynanchoides*, but must be considered a species on morphological criteria.

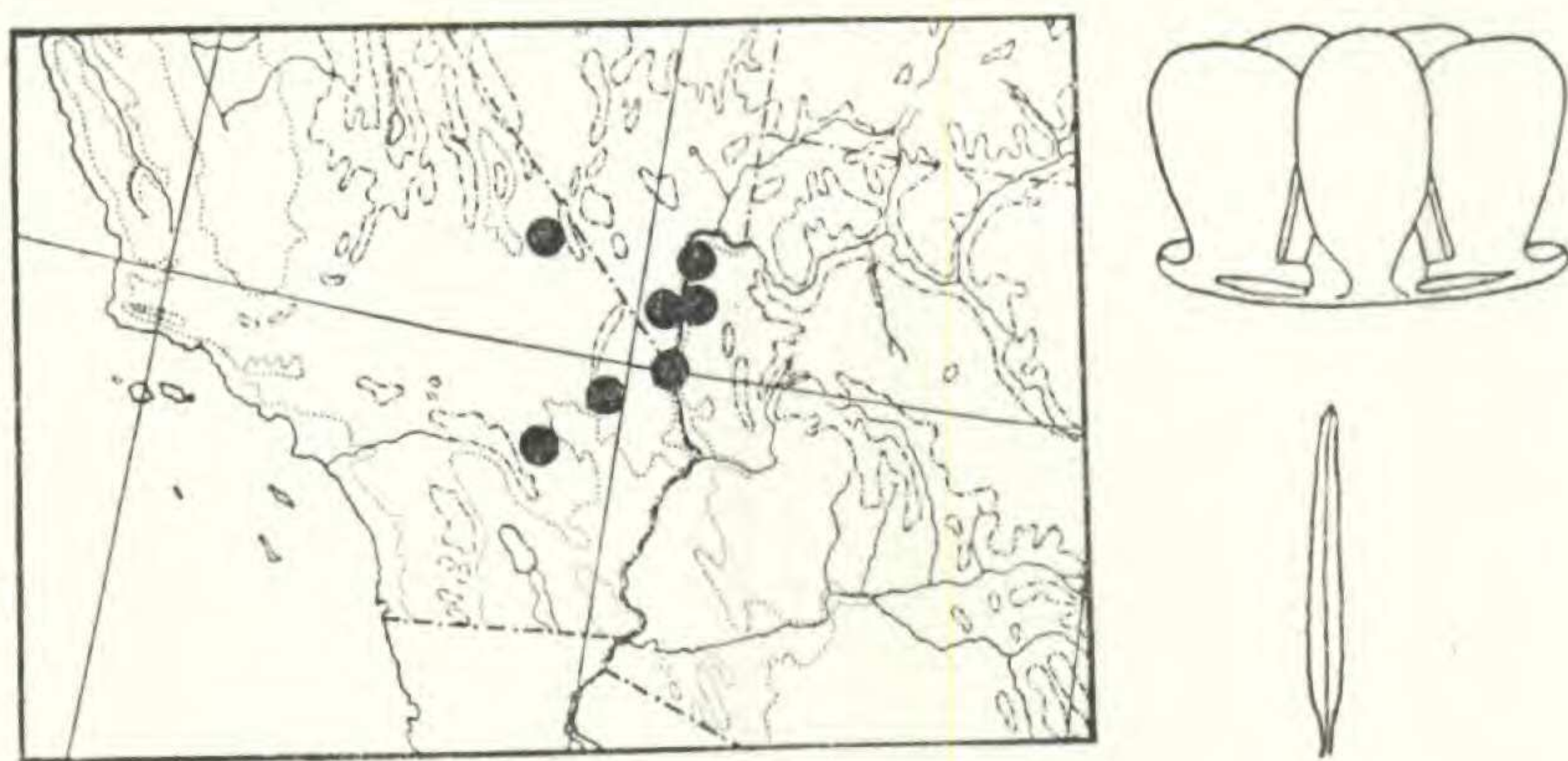


Fig. 14. Distribution, gynostegium, and leaf of *S. birtellum*.

*Sarcostemma birtellum* occurs at altitudes of from 450 to 3500 feet. It is an undershrub several feet in height, but creeping branches may extend several feet along the sandy or rocky soil of the ravines of washes in which it grows. While the aerial stems are slender and herbaceous, there is a large, woody caudex at the base and a series of very stout, deeply penetrating roots. The crushed herbage has an odor pronouncedly sudoral or reminiscent of garlic. Blooming dates range from March 26 to May 5; one specimen was collected in flower in October. Follicles are produced from April to May.

UNITED STATES. NEVADA: CLARK CO.: 14 miles E of Searchlight, *Train 1283*; Mike Tobins, *Thackery 333*. ARIZONA: MOHAVE CO.: 7 miles S of Boulder Dam, *Peebles & Parker 14785*; YUMA CO.: Buckskin Mts., *Keck 4345*. CALIFORNIA. CALAVERAS CO.: Vallecito, *Orcutt 2250*; RIVERSIDE CO.: Corn Springs, *C. L. Hitchcock 12199*; SAN BERNARDINO CO.: near Needles, *Macbride & Drouet 4453*; SAN DIEGO CO.: San Felipe Canyon, *Eastwood 2780*.

12. *SARCOSTEMMA ARENARIUM* Decne. ex Benth. Bot. Voy. Sulph. 34. 1844. (T.: *Hinds 1841 in Herb. Kew.*!).

Stems twining or trailing, very thick at the base and with much ridged bark, gray-green above, puberulent, the nodes densely white-pubescent; lateral branches many and long at the base, few above. Leaves more or less caducous, narrowly oblanceolate, obtuse, cuneate, 3.5 cm. long, 0.3–0.8 cm. wide, coriaceous, somewhat revolute when dried, sparsely pilose above and beneath with small glands on the midrib at the base; petiole 0.05–0.1 cm. long. Inflorescences umbelliform, 6- to 12-flowered; peduncle 2.2–3.5 cm. long, rarely equalling the subjacent inter-



node in thickness, pilose; bracts linear, 0.1–0.2 cm. long; pedicels 1.0–1.3 cm. long, densely pilose. Calyx lobes narrowly lanceolate, 3 mm. long, involute, pilose without, glabrous within; squamellae alternate, usually solitary, relatively long. Corolla rotate-subcampanulate, the tube 2.5–3.0 mm. long, the lobes ovate, obtuse, 4.5–6.0 mm. long, pilose without, puberulous-papillate within, ciliate. Gynostegium 2.5–3.0 mm. high, the column 1 mm. long. Anthers 1 mm. long, the apical appendage deltoid, the pollinium-sacs clavate-oblongoid, 0.5 mm. long, with narrowly sagittate corpusculum; ring of the corona prominent, somewhat revolute, adnate to the column; vesicles of the corona spherical to oblongoid, 1.0–1.5 mm. long. Ovaries 2 mm. long, rather densely pilose; stigma-head obscurely bilobed, convex. Follicles narrowly obclavate, attenuate, 6.4 cm. long, 0.9 cm. thick, puberulent; seeds unequally biconvex, 7 mm. long, 3 mm. wide, obscurely rugose dorsally, minutely papillate ventrally; coma about 3 cm. long.

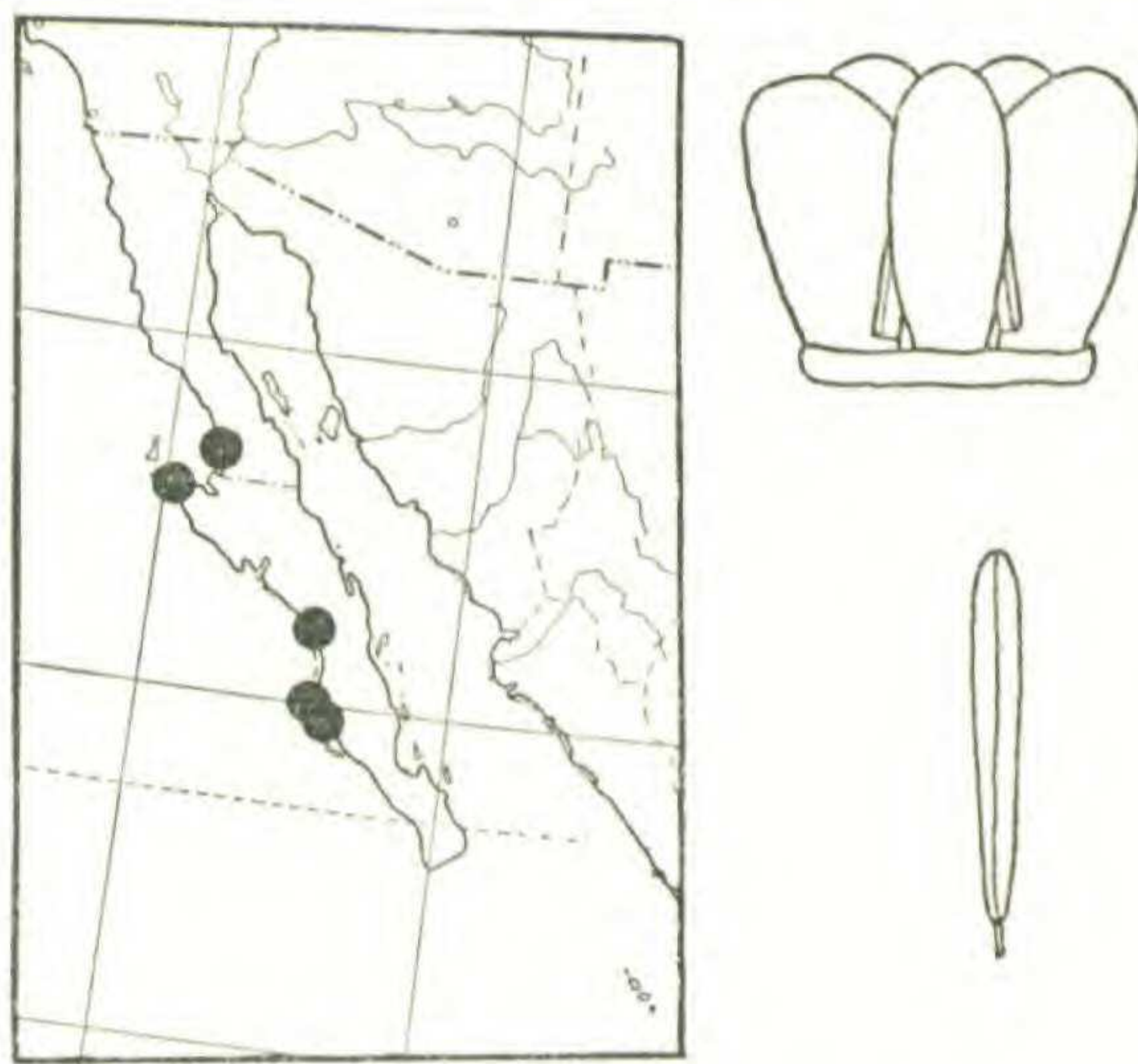


Fig. 15. Distribution, gynostegium, and leaf of *S. arenarium*.

A poorly understood species endemic to the western coast of Baja California. *Sarcostemma arenarium* has been confused with *S. cynanchoides* *Hartwegii* and *S. birtellum*, from both of which, however, it is rather easily distinguished by its oblanceolate leaves, larger flowers, and densely pubescent calyx. In many respects it is fairly close to *S. clausum*, and may perhaps represent an offshoot of that variable stock. If so, it has diverged so far in the direction of ser. CYNANCHOIDES as to make any statements concerning its relationships very tenuous.

MEXICO. BAJA CALIFORNIA SUR: San Bartolomé Bay, *Rose 16214*; Magdalena Bay, *Mason 1929*, *Hinds 1841*, TYPE; Magdalena Island, *Orcutt 31*, *Brandege 1889*; Lagoon Head, *E. Palmer 814*; San Juanico, *Gentry 4297*.

Series 4. ANGUSTISSIMA R. Holm, ser. nov.

Inflorescentia vere terminalis umbelliformis, pedunculo quam internodio subjacenti angustiore (interdum obsoleto).

Type species: *Sarcostemma angustissimum* (Anderss.) R. Holm.



This monotypic series includes a single species, endemic to the Galapagos Islands, which differs from other members of the genus in having a truly terminal inflorescence.

13. *SARCOSTEMMA angustissimum* (Anderss.) R. Holm, comb. nov.

*Asclepias angustissima* Anderss. Galap. Oarnes Veg. 196. 1853. (T.: *Andersson s. n. in Herb. Stockholm!*).

*Funastrum angustissimum* (Anderss.) Fourn. in Ann. Sci. Nat. Bot. VI, 19:388. 1882.

Stems twining or semi-erect, green, glabrous; lateral branches many. Leaves oblanceolate, linear, acute, cuneate, 2.5–4.5 cm. long, 0.1–0.3 cm. wide, subcoriaceous, revolute when dried, glabrous above and beneath, without glands on the midrib at the base; petiole 0.1–0.2 cm. long. Inflorescences umbelliform, terminal to the main axis or lateral branches, 7- to 15-flowered; peduncle 0–1 cm. long, very minutely pilosulose, not equalling the subjacent internode in thickness; bracts linear, minute; pedicels 0.5–1.5 cm. long, very minutely pilosulose. Calyx lobes ovate, 1.5 mm. long, hispidulous without, glabrous within, ciliolate, the apex glandular; squamellae absent. Corolla rotate-subcampanulate, black when dried, the tube 1.25 mm. long, the lobes ovate, acute, 2.5 mm. long, glabrous on both surfaces. Gynostegium 2 mm. high, the column very short. Anthers 1 mm. long, the apical appendage semi-orbicular, the pollinium-sacs oblongoid, 0.5 mm. long, with sagittate corpusculum; ring of the corona thin, scarcely adnate to the base of the corona vesicles; vesicles of the corona ovoid-oblongoid, pointed at the tip, 2 mm. long. Ovaries 1 mm. long, very minutely pubescent; stigma-head convex, entire. Follicles apparently narrowly fusiform, about 9 (?) cm. long; seeds unknown.

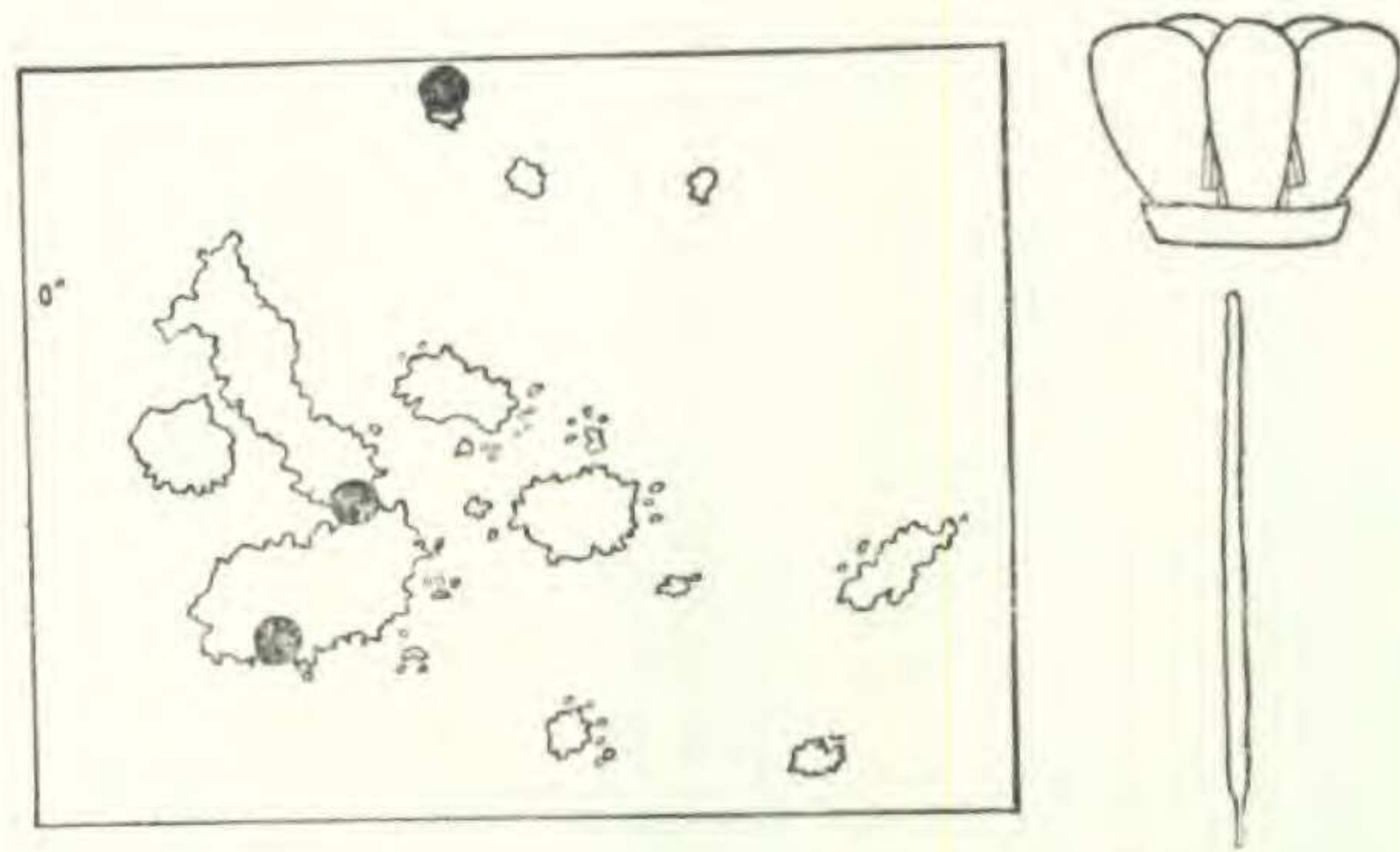


Fig. 16. Distribution, gynostegium, and leaf of *S. angustissimum*.

The small, dark flowers of this Galapagos Island endemic are quite distinctive, as are the terminal inflorescences. Little can be said about the relationships of *S. angustissimum* since it has been so rarely collected and is so reduced morphologically. Apparently it flowers from January to June.

GALAPAGOS ISLANDS. ABINGDON IS.: *Snodgrass & Heller 845*. ALBEMARLE IS.: *Andersson s. n.*, TYPE; Tagus Cove, *Snodgrass & Heller 145*.



## Series 5. FLAVA R. Holm, ser. nov.

Coronae annulus obsoletus.

Type species: *Sarcostemma flavum* Decne.

A monotypic series including a species of the Río de la Plata area of South America. The ring of the corona is entirely lacking, immediately separating this species from all others in the subgenus.

14. *SARCOSTEMMA FLAVUM* Decne. in DC. Prodr. 8:540. 1844. (T.: *D'Orbigny s. n. in Herb. Paris.*!).

*Philibertia stellaris* Griseb. Symb. Fl. Arg. 234. 1879, ex char.

*Cystostemma umbellatum* Fourn. in Mart. Fl. Bras. 6<sup>4</sup>:204. 1885. (T.: *St. Hilaire s. n.*!).

*Ceramanthus flavus* (Decne.) Malme in Ark. Bot. 4<sup>14</sup>:2. 1905.

*Philibertia longifolia* Arech. in Ann. Mus. Nac. Montevideo 4:87. 1909, ex char.

*Funastrum flavum* (Decne.) Malme, in Bull. Soc. Bot. Genève. II, 3:269. 1911.

*Funastrum longifolium* (Arech.) Schltr. in Fedde's Repert. 13:286. 1915.

Stems twining, green, pilosulose; lateral branches few. Leaves long, lanceolate, acuminate to acute, cordate, the lobes descending, 7.0–12.5 cm. long, 3.5–4.0 cm. wide, subcoriaceous, appressed-pilose above, densely so beneath, with several glands on the midrib at the base; petiole 1.5–2.0 cm. long. Inflorescences umbelliform, the floriferous axis slightly manifest, 9- to 15-flowered; peduncle 4.5–14.0 cm. long, pilosulose; bracts linear, minute; pedicels 5–10 cm. long, pilose. Calyx lobes narrowly lanceolate, 2.5 mm. long, copiously puberulent without, glabrous within; squamellae 3–7, alternate. Corolla rotate-subcampanulate, the tube 0.9 mm. long, the lobes broadly ovate, 4 mm. long, glabrescent without, glabrous within. Gynostegium 2.5 mm. high, the column obsolete. Anthers 1.5 mm. long, the apical appendage deltoid, obscurely emarginate, the pollinium-sacs oblongoid-cylindrical, 0.5 mm. long, with ellipsoid to obscurely sagittate corpusculum; ring of the corona lacking; vesicles of the corona ovoid, the inner side more or less apiculate at the tip, 2.5 mm. long. Ovaries 1.5 mm. long, glabrous; stigma-head obscurely bilobed. Follicles and seeds unknown.

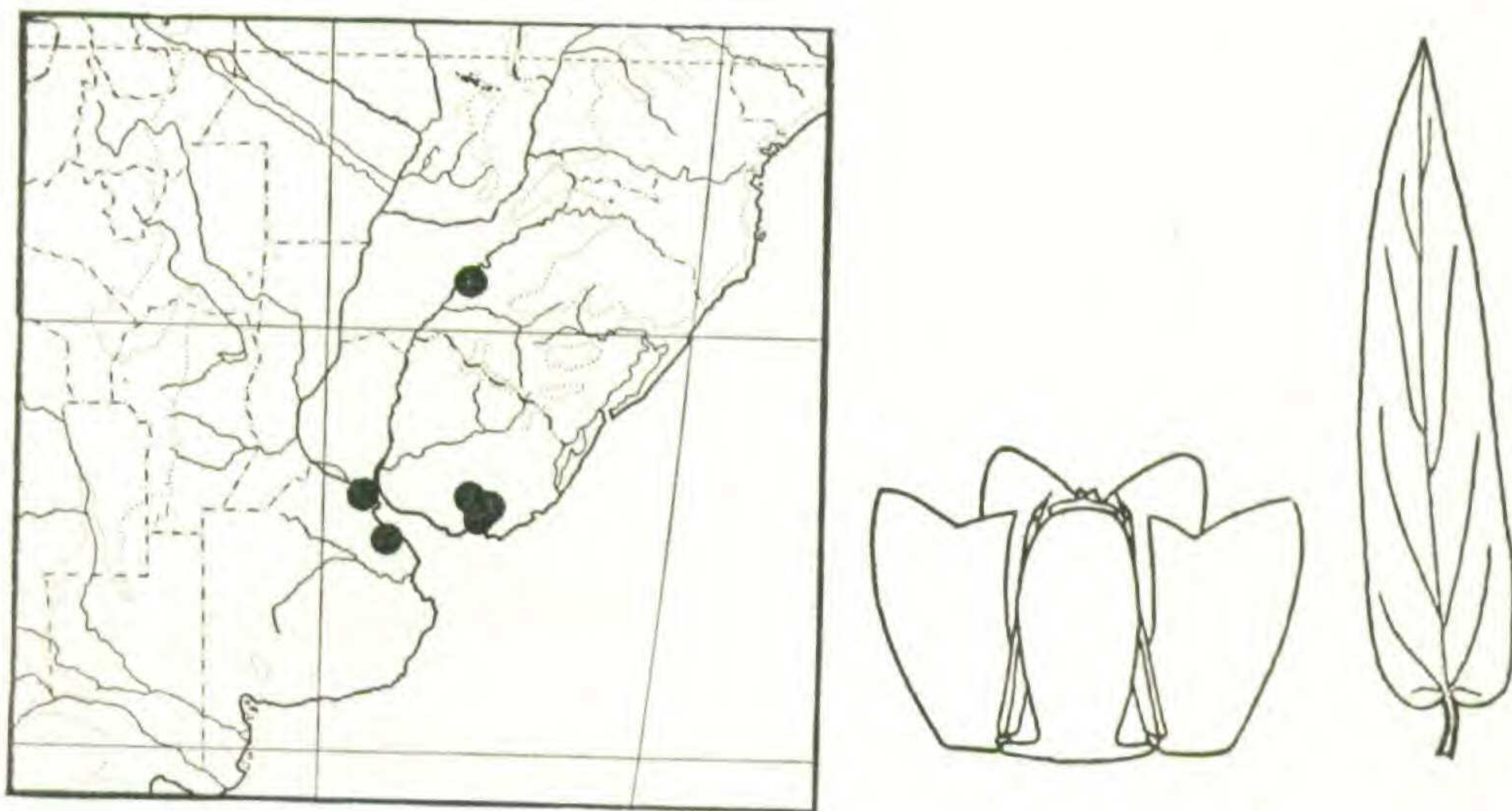


Fig. 17. Distribution, gynostegium, and leaf of *S. flavum*.



This distinctive species apparently is rare, for few specimens have been available for study. The lack of the ring of the corona and the disproportionate length of the leaves form good characters. One of the few species which occurs in lowland areas, it inhabits the borders of the Paraná and Plata rivers. Only the type specimen and the material from the Naturhistoriska Riksmuseet, Stockholm, have been available, so that most of the distribution records are taken from the monograph of the Argentine species of *Funastrum* and *Philibertia* by T. Meyer.<sup>56</sup> The species ranges from southern Brazil to adjacent Argentina and Uruguay.

BRASIL. RÍO GRANDE DO SUL: *St. Hilaire* s. n., type of *C. umbellatum* Fourn.

URUGUAY. CANELONES: near the Río de la Plata, *Legrand* 34. CERRO LARGO: Cerro de las Cuentas, *Rosengurtt* 2773. SAN JOSÉ: Barra, *Herter* 738; Santa Lucía, *Arechaveleta* s. n.

ARGENTINA. BUENOS AIRES: Conchitas, orillas del Río de la Plata, *Hauman* s. n.; delta del Paraná, *Hauman* s. n. ENTRE RÍOS: Río Bravo, *Kuschel* 532, 533, 534.

Subgenus II. OXYSTELMA (R. Br.) R. Holm, stat. nov.

*Oxystelma* R. Br. in Mem. Wern. Soc. 1:40. 1809.

*Philibertia* HBK. Nov. Gen. et Sp. Pl. 3:195. 1819.

*Pentagonium* Schauer, in Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1:364. 1843.

*Lugonia* Wedd. Chlor. And. 2:49. 1857.

*Zosima* Phil. Sert. Mend. Alt. 29. 1871, non Hoffm.

*Pentacyphus* Schltr. in Engl. Bot. Jahrb. 37:605. 1906.

*Tetraphysa* Schltr. loc. cit. 616. 1906.

Leaves laminate; inflorescences racemiform or umbelliform; corolla subrotate-campanulate to campanulate, ring of the corona adnate to the corolla or more or less obsolete.

Type species: *Sarcostemma esculentum* (L.) R. Holm.

The species of this subgenus are South American plants of Andean affinities, except for the Old World *S. esculentum* which occurs in Africa and Asia. Because of the close similarity in vegetative structure between the various species, it has been necessary to place a greater emphasis on characters of the gynostegium in the keys. In every case, however, examination of the dried flowers should suffice for identification; drawings are provided to illustrate the typical condition for each species.

#### KEY TO THE SECTIONS

A. Vesicles of the corona ovoid to subspheroid, obtuse at the apex or abruptly constricted to form a short apical process, never exceeding the stigma-head in length; ring of the corona glabrous or obsolete; column glabrous; translator arms well-developed. Species of the Western Hemisphere.

B. Corolla lobes acute or acuminate, the tube free from the column (partly adnate in *S. lysimachioides*), glabrous within; gynostegium not highly vernicose, the column terete or ribbed, not deeply grooved; inflorescences racemiform or umbelliform, consisting of many 1- to 2-flowered cymules (occasionally indicated only by their bracts or reduced to one).....

Section 1. PHILIBERTIA (Spp. 15-20)

<sup>56</sup>Meyer, T. In Lilloa 9:428. 1943.



- BB. Corolla lobes broadly obtuse, the tube adnate to the column directly below the anthers, pubescent within forming five hairy pouches alternating with the stamens; gynostegium highly vernicose, the column longitudinally grooved between the stamens, the margins of the groove produced and arrect, continuous with the anther wings; inflorescence racemiform, consisting of 2 1-flowered cymules, or umbelliform. ....Section 2. PENTACYPHUS (Spp. 21-22)
- AA. Vesicles of the corona ovoid, gradually constricted above into a long, incurved process, exceeding the stigma-head in length; ring of the corona pubescent; column pubescent; translator arms obsolete. Species of the Eastern Hemisphere. ....Section 3. EUOXYSTELMA (see p. 482)

Section 1. PHILIBERTIA (HBK.) Decne. in DC. Prodr. 8:541. 1844.

The majority of the species in the subgenus OXYSTELMA belong to this group of forms of undoubted close relationship. All appear to be more or less localized in distribution, in contrast to the species of subg. CERAMANTHUS or EUSARCOSTEMMA, except for *S. Gilliesii* of Argentina and Bolivia. As a rule, they may be recognized easily by the campanulate corolla, the glabrous gynostegium with scarcely apparent corona ring, and the few-flowered inflorescence.

KEY TO THE SPECIES

- a. Plants usually climbing, very rarely semi-erect; corolla tube free from the column.
- b. Corolla broadly and shallowly campanulate; vesicles of the corona equalling or somewhat exceeding the anthers (rarely reduced in aberrant individuals, cf. *S. Gilliesii*); pollinia rounded, clavate-cylindrical, fertile to the attachment of the translator arm, the corpusculum sagittate.
- c. Vesicles of the corona narrowly ovoid-oblongoid, with a vertical ventral keel, gradually decurrent upon the column, the gynostegium somewhat longer than broad; sepals reflexed, corolla 2-3 cm. broad. ....15. *S. campanulatum*
- cc. Vesicles of the corona truncate-oblongoid or ovoid to spheroid, not decurrent upon the column, the gynostegium usually broader than long; sepals ascending, corolla 0.8-1.0 cm. broad, rarely to 2 cm. broad.
- d. Inflorescences racemiform to corymbiform, obviously compound; stigma-head usually 2-apiculate; vesicles of the corona narrowly ovoid or obovoid to subspheroid, with a more or less pronounced apical appendage, constricted at their insertion upon the column.
- e. Vesicles of the corona widest below the middle, the gynostegium uniformly light in color; corolla with purple markings within. ....16. *S. Gilliesii*
- ee. Vesicles of the corona widest above the middle, light in color, the column and anthers very dark; corolla usually uniformly light in color. ....17. *S. Vaileae*
- dd. Inflorescences umbelliform, the pedicels all inserted at nearly the same point; stigma-head umbonate or broadly 2-lobed; vesicles of the corona truncate-oblongoid, scarcely constricted at their insertion upon the column. ....18. *S. solanoides*
- bb. Corolla urceolate-campanulate; vesicles of the corona about one-third to one-half the length of the anthers; pollinia flattened, clavate, with a sterile hyaline region at the attachment of the translator arm, the corpusculum narrowly ellipsoid. ....19. *S. stipitatum*
- aa. Plants prostrate, the branches trailing from a short woody caudex; corolla tube adnate to the column directly below the anthers. ....20. *S. lysimachioides*



15. *SARCOSTEMMA CAMPANULATUM* Lindl. Bot. Reg. n. s. 9, t. 36. 1846. (T.: Hort. Veitch. in Herb. Univ. Cantab.!).

*Philibertia campanulata* (Lindl.) Nichols. Dict. Gard. 3:96. 1886.

*Philibertia hypoleuca* Schltr. in Oesterr. Bot. Zeitschr. 45:450. 1895. (T.: Kunze s. n. in Herb. Berol.).

*Philibertia splendens* Lillo, in Physis 4:429. 1919. (T.: Lillo 7350 in Herb. Lillo!).

*Philibertia speciosa* Malme, in Ark. Bot. 26A<sup>4</sup>:32. 1935, *sphalm*.

Stems twining, minutely pilosulose in lines decurrent from the petioles; lateral branches few. Leaves lanceolate, acuminate, rather deeply cordate, the lobes descending, 3.5–8.0 cm. long, 1.0–4.8 cm. wide, firmly membranaceous, glabrate to minutely puberulent above, subtomentose to tomentose beneath, with one or more glands on the midrib at the base; petiole 1.0–4.2 cm. long. Inflorescences racemiform, 2- to 9-flowered; peduncle 0.7–7.8 cm. long, appressed-pilosulose; bracts linear, 0.2–0.3 cm. long; pedicels 1.1–2.4 cm. long, appressed-pilosulose. Calyx lobes narrowly lanceolate, reflexed, 4 mm. long, puberulous-pilose on both surfaces; squamellae few, alternate. Corolla campanulate, greenish yellow to cream with red or purple spots or streaks within, the tube 8 mm. long, the lobes acute to acuminate, 5 mm. long, pilosulose without, glabrous within. Gynostegium 5–6 mm. high, the column 2 mm. long. Anthers 1.5 mm. long, the apical appendage deltoid, the pollinium-sacs clavate-cylindrical, 0.5 mm. long, with broadly sagittate corpusculum; ring of the corona very short; vesicles of the corona narrowly oblongoid, the ventral face constricted longitudinally to form a vertical keel, gradually decurrent upon the column, 2 mm. long (rarely much reduced). Ovaries 2 mm. long, sparsely puberulent; stigma-head cylindrical, with a long 2- or 3-fid apiculation. Follicles and seeds unknown.

*Sarcostemma campanulatum* is distinguished from all other species of the genus by the structure of the gynostegium. Here the corona vesicles are constricted longitudinally along the ventral face so that a vertical ventral keel is produced; there is no terete appendage such as is found in many species. Dorsally, the corona vesicles are decurrent upon the column to the corolla. It is noteworthy that the anther wings are usually broad and cartilaginous, while the pollinia are stout and short and connected by broad, sagittate corpuscula. A peculiar variant, which has been collected several times in the Cuzco region in Peru, has corona vesicles which are shrunken and more or less linear in outline. The gynostegium nevertheless is clearly that of *S. campanulatum*. As a rule in this form, the leaves are decidedly more tomentose beneath and the sepals are less strongly reflexed.

It is by virtue of the long, racemiform inflorescence and relatively unbranched habit, coupled with the large size, that *S. campanulatum* is assigned the primary position in the section. The relationships in subg. *OXYSTELMA* are, in general, much less clear than those in subg. *CERAMANTHUS*, so that this position in the sequence of species is based primarily on the general impression given by the plant, rather than upon any rigorous or dogmatic treatment of morphological criteria.



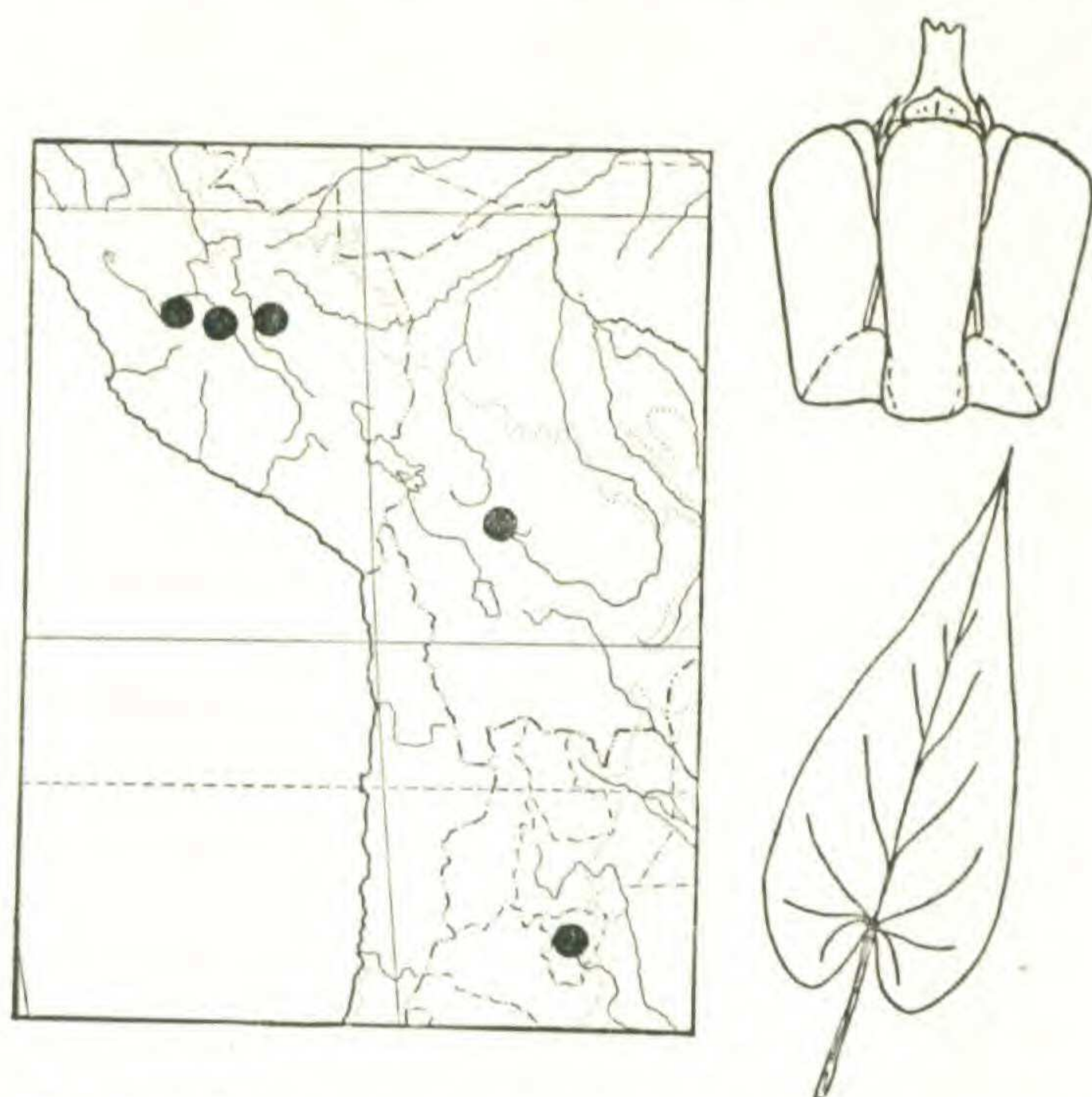


Fig. 18. Distribution, gynostegium, and leaf of *S. campanulatum*.

*Sarcostemma campanulatum* is a stout vine climbing to heights of four meters in small trees and shrubs. Apparently it grows in relatively moist locations in woods and occasionally in cultivated ground, at altitudes from 6000 to 11000 feet in the Peruvian and Bolivian Andes. The specimens from Tucumán, Argentina, are rather inexplicable. The species has been collected in flower from December to March, and in fruit in April.

PERU. APURIMAC: Abancay, Labrama, Matara Canyon, Vargas 9801; Abancay, Ampuy, Stork, Horton & Vargas 10953; Abancay, Labrama, Vargas 1426; Abancay, Mariño, Vargas 1459. CUZCO: Anta, Vargas 204; Colca, Vilcabamba, Vargas 4013; Paruro, entre Huachachacca i Huanca-Huanca, Vargas 2387. HUANCAVELICA: Tayacaja, Ampurco, Weberbauer 6503; Tayacaja, 3 km. N of Salcabamba, Stork & Horton 10318.

BOLIVIA. COCHABAMBA: Tunari, Kuntze s. n., type of *P. hypoleuca* Schltr.

ARGENTINA. TUCUMÁN: Tafí, La Angostura, Castellón 2034; Chicligasta, Estancia Las Pavas, Venturi 6458.

16. *SARCOSTEMMA GILLIESII* (H. & A.) Decne. in DC. Prodr. 8:542. 1844.

*Philibertia Gilliesii* Hook. & Arn. in Hook. Lond. Jour. Bot. 1:290. 1834. (T.: Tweedie s. n. in Herb. Kew!).

*Philibertia grandiflora* Hook. in Bot. Mag. 64, t. 3618. 1837. (T.: Tweedie s. n. in Herb. Kew!).

*Philibertia gracilis* D. Don in Sweet, Brit. Fl. Gard. II, 4: t. 403. 1838. (T.: Tweedie s. n. in Herb. Kew.).

*Sarcostemma Donianum* Decne. loc. cit. 1844.

*Sarcostemma grandiflorum* (Hook.) Decne. loc. cit. 1844.

*Sarcostemma incanum* Decne. loc. cit. 1844. (T.: D'Orbigny 246 in Herb. Paris!).

*Amblystigma pedunculare* Benth. in Hook. Ic. Pl. 32:77. 1846. (T.: Mandon 353 in Herb. Kew!).

*Zosima violacea* Phil. Sert. Mend. Alt. 29. 1871. (T.: Philippi s. n.).

*Oxystelma Gilliesii* (H. & A.) K. Schum. in E. & P. Natur. Pflanzenfam. 4<sup>2</sup>:229. 1895.

*Oxystelma violacea* (Phil.) K. Schum. loc. cit. 1895.



- Philibertia Gilliesii* H. & A. var. *pubescens* Speg. in Anal. Soc. Cient. Argent. 53:72. 1902, ex char. (T.: *Spegazzini s. n.*).
- Philibertia violacea* (Phil.) Schltr. in Fedde's Repert. 13:283. 1915.
- Philibertia Gilliesii* H. & A. var. *albida* Stuck. ex Seckt. Rev. Univ. Nac. Córdoba 17<sup>5-6</sup>:70. 1930, ex char.
- Philibertia Gilliesii* H. & A. var. *vestita* Malme, Ark. Bot. 26A<sup>4</sup>:36. 1934, ex char.
- Philibertia grandiflora* Hook. f. *albida* Malme, loc. cit. 34. 1934, ex char. (T.: *Stuckert 13822 in Herb. Lillo*).
- Philibertia Gilliesii* H. & A. var. *grandiflora* (Hook.) T. Meyer, in Lilloa 9:452. 1943.
- Philibertia Gilliesii* H. & A. var. *gracilis* (D. Don) T. Meyer, loc. cit. 1943.
- Philibertia Gilliesii* H. & A. var. *parvicoronata* T. Meyer, loc. cit. 453. 1943. (T.: *Meyer 4117 in Herb. Lillo*!).
- Philibertia Schreiteri* T. Meyer, loc. cit. 436. 1943. (T.: *Schreiter 4540 in Herb. Lillo*!).
- Philibertia Gilliesii* H. & A. var. *mirabilis* T. Meyer, in Descole, Gen. et Sp. Pl. Argent. 2:173. 1944. (T.: *Meyer 5112 in Herb. Lillo*!).

Stems twining to rarely semi-erect, minutely puberulent in lines decurrent from the petioles; lateral branches many. Leaves narrowly lanceolate to ovate, acuminate to acute, deeply cordate, the lobes descending to converging, 2.5–4.0 cm. long, 0.3–3.2 cm. wide, membranaceous, revolute, glabrate to rather densely pilose on both surfaces, with one or more glands on the midrib at the base; petiole 1.0–2.5 cm. long. Inflorescences racemiform, 2- to 7-flowered; peduncle 1–5 cm. long, minutely puberulent; bracts linear, 0.1–0.2 cm. long; pedicels 1.0–2.5 cm. long, minutely puberulent. Calyx lobes narrowly lanceolate, 2.5 mm. long, pilosulose without, glabrous within; squamellae alternate and few, or many and indefinitely distributed within the calyx. Corolla campanulate, greenish yellow to cream with red or purple spots or streaks within, the tube 6–9 mm. long, the lobes acute to acuminate, 1.5–2.0 mm. long, glabrous to pilosulose without, glabrous within. Gynostegium 3 mm. high, the column 1 mm. long. Anthers 1.0–1.5 mm. long, the apical appendage rhomboidal, the pollinium-sacs clavate-cylindrical, 0.5 mm. long with sagittate corpusculum; ring of the corona obsolete; vesicles of the corona ovoid to subspheroid, abruptly constricted at the apex to form a more or less pronounced apiculation, abruptly constricted at their insertion upon the column, 1.5 mm. long. Ovaries 2 mm. long, glabrous; stigma-head cylindrical, 2-apiculate, the apiculae often flattened and reflexed. Follicles about 3.5 cm. long, 0.7 cm. thick; seeds unknown.

In many respects *Sarcostemma Gilliesii* is the counterpart, in subg. OXYSTELMA, of *Sarcostemma* (CERAMANTHUS) *clausum*. I have considered it to be a polytypic species which has developed a number of races, apparently in response largely to increasing aridity. These populations, however, do not appear to be sufficiently distinct to be classified even as subspecies and therefore are not recognized nomenclaturally. The element known as *Philibertia gracilis* is, for the most part, northern (Bolivia and adjacent Argentina), and is a slender vine with broad, cordate, membranaceous, and glabrous leaves. In the southern provinces of Argentina is the so-called variety *pubescens* of *P. Gilliesii*, with narrow, hastate, subcoriaceous, and densely pubescent leaves. More or less intermediate geographically and morphologically (but broadly overlapping at both extremes) is the typical *S. Gilliesii*.



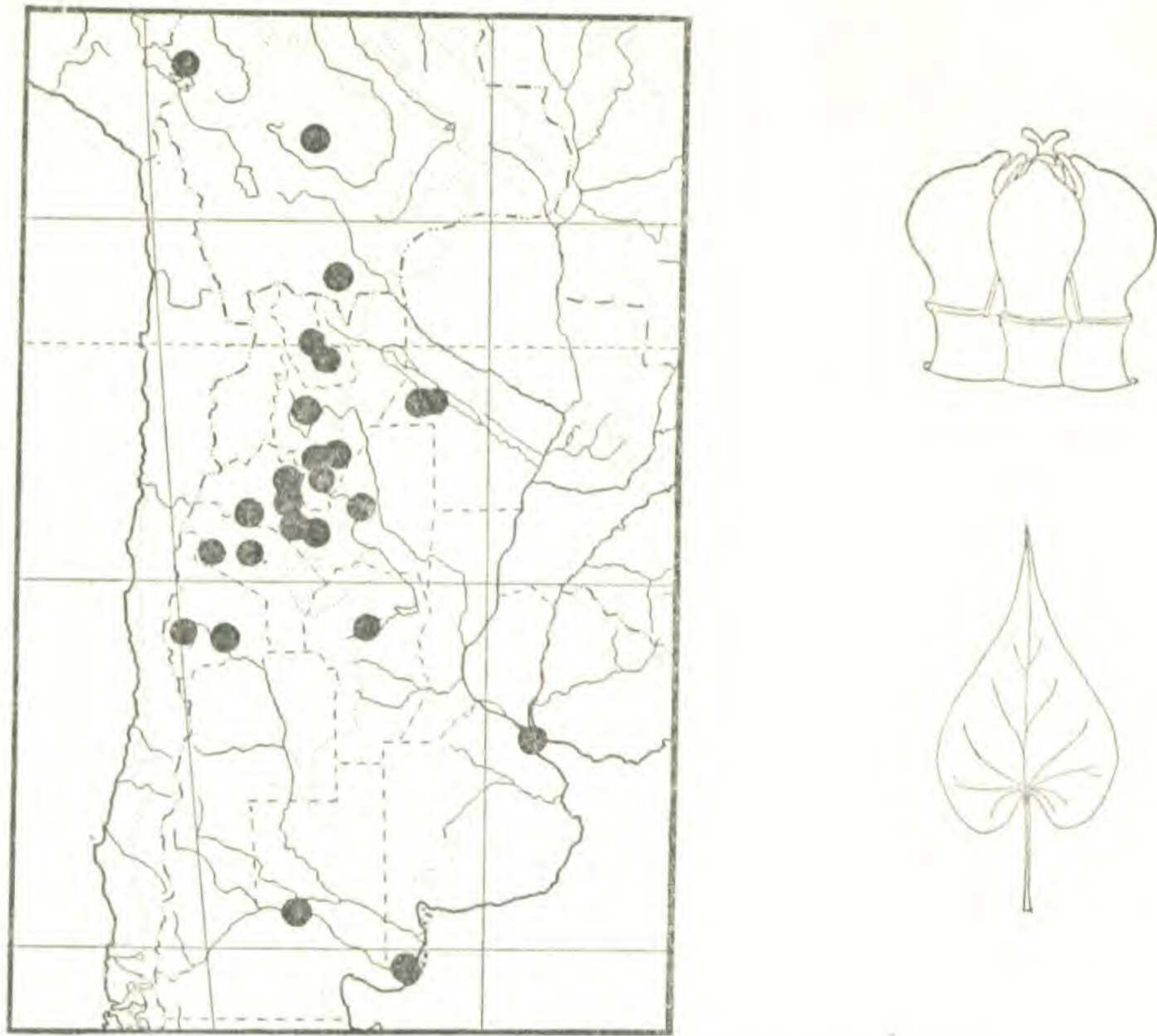


Fig. 19. Distribution, gynostegium, and leaf of *S. Gilliesii*.

There are also several local variants which are of interest: var. *parvicoronata* of T. Meyer includes those relatively common, but by no means distinct, forms in which the corona vesicles are shrunken and linear in outline; *P. Schreiteri* Meyer is a form with follicles of such a degree of rugosity that they appear squamate; *P. grandiflora* Hook. has larger flowers and lanceolate leaves rather more pubescent beneath than above. Except for the characters mentioned, these variants possess all of the attributes of *Sarcostemma Gilliesii*. Whether they are to be recognized as varieties is a matter of preference which should, however, be based upon experience with the genus as a whole. I prefer not to do so until population studies can be made. I can find no altitudinal, habitat, or flowering period differences among the various subgroups of *S. Gilliesii*, except for the obvious fact that those from the more southern stations experience greater aridity.

*Sarcostemma Gilliesii* is a sub-shrub of twining to trailing habit. Like other desert species of the genus, it makes tangled masses several feet in diameter, climbing over rocks and shrubs, as well as itself, in dry, rocky soil. Occasionally it may climb into trees. It grows at altitudes from 450 to 3000 feet and has been collected in flower from September to March. I have seen no fruit, except for a single distorted follicle collected in August. An interesting specimen was collected among ballast at Karghus Point, New Jersey. According to the collector, Dr. Henry Leffmann, in a letter to Asa Gray, it was a perennial which flowered abundantly but did not fruit.



BRAZIL (?): Río Negro, D'Orbigny 246, type of *S. incanum* Decne.

BOLIVIA. COCHABAMBA: quebradas de Totara, Steinbach 5992; near Yungas, Rusby 1973. LA PAZ: near Sorata, Mandon 353, type of *Amblystigma pedunculare* Benth. TARIJA: near Tarija, Fiebrig 2668.

ARGENTINA. BUENOS AIRES: Monte Hermoso, Carette s. n.; island near Buenos Aires, Tweedie s. n.; Isla Martín García, Cabrera 2846. CATAMARCA: Capital, Alta Chaya, Castillón 1071; El Cajon, Las Visacheras, Castillón 3349; Pomán, near Pomán, Castillón 1029 (part); Ambato, El Potrero, Castillón 1069; Capital, Castillón 1072, 1958; Valle de Santa Maria, Punto de Balasto, Schreiter s. n.; Andalgalá, Andalgalá, Jörgensen 1095; Tinogasta, Vallecito a Agua Negro, Schreiter 6284; Ambato, El Rodeo, Castillón s. n. CHACO: Nueva Pompeya, Jörgensen 3025. CÓRDOBA: Córdoba, Río II, Stuckert 23264; Malagueño, Bartlett 20069; near La Falda, Job 515; Kuntze s. n., Stuckert s. n., Lössen 39. FORMOSA: Guayculec, Jörgensen 3184. JUJUY: Tilcara, Cerro Peña, Venturi 4939; Tilcara, Maimara, Hualchin, Budin s. n.; Humahuaca, quebrada de Humahuaca, El Volcán, Castillón 6421; Volcán, Loma de Laguna, Schreiter 2590; Tilcara, quebrada de Euasamayo, E. K. Balls B5962. LA RIOJA: Famatina, Famatina, T. Meyer 4255; General Lavalle, Guandacol, T. Meyer 4182. MENDOZA: Pampa de St. Rafael, Wilczek 281; Maipu, Barrancas, Bartlett 19335; Potrerillos, Bartlett 19325; between Villaviciencia and Uspullata, Senn 4452. RÍO NEGRO: vicinity of General Roca, Fischer 110. SALTA: San José, Lorentz & Hieronymus 221; Capital, Salta, Hunziker 2722. SANTIAGO DEL ESTERO: Gramilla, Venturi 10281. TUCUMÁN: Trancas, Tapia, Schreiter 3495; Río Chico, La Cocha, Bailetti 148, 350, 545; Trancas, Raco, Venturi 1202; Trancas, Chaspiyacu, Schreiter 5514; Capital, Lillo 320, 11864; Tafi, Amaicha, Castillón 2485, Schreiter 5511; Trancas, Tapia, Venturi 1114, Lillo 4840, Rodriguez 596; Trancas, Vipos, Venturi 1717, Schreiter 4540, type of *P. Schreiteri* Meyer; Burruyacu, Cerro del Campo, Venturi 7720; Capital, Villa Luian, Venturi 280; Capital, Barranca Colorada, Venturi 4095; Tafi, La Casita, region del Aliso, Lillo 7350; Burruyacu, Cerro de Durasnillo, Monetti 1992; Tucumán, Tweedie s. n., type of *P. grandiflorum* Hook.

17. *SARCOSTEMMA Vaileae* (Rusby) R. Holm, comb. nov.

*Oxystelma Vaileae* Rusby, in Bull. N. Y. Bot. Gard. 4:315. 1907. (T.: Bang 985 in Herb. N. Y. Bot. Gard.!).

*Philibertia albiflora* Lillo, in Physis 4:428. 1919. (T.: Castillón 9463 in Herb. Lillo!).

Stems twining, minutely pilosulose in lines decurrent from the petioles; lateral branches many. Leaves deltoid-lanceolate, acute to obtuse, shallowly cordate, the lobes descending or diverging, 2.9–7.0 cm. long, 0.8–2.9 cm. wide, glabrate to minutely pilosulose above, glabrate to subtomentose beneath, with one or more glands on the midrib at the base; petiole 1.9–2.9 cm. long. Inflorescences racemiform, 2- to 7-flowered; peduncle 1–5 cm. long, minutely pilosulose; bracts linear, 0.1–0.2 cm. long; pedicels 1.0–2.5 cm. long, minutely pilosulose. Calyx lobes narrowly lanceolate, 3 mm. long, pilosulose without, scatteringly pilosulose within; squamellae numerous, indefinitely distributed within the calyx. Corolla campanulate, yellowish green to cream-colored, the tube 6 mm. long, the lobes acute, 2.5–3.0 mm. long, pilosulose without, glabrous within. Gynostegium 3 mm. high, the column 0.75 mm. long. Anthers 1.5 mm. long, the apical appendage rhomboidal, the pollinium-sacs clavate-oblongoid, 0.5 mm. long, with sagittate corpusculum; ring of the corona nearly obsolete; vesicles of the corona obovoid-oblongoid, with a short apical appendage, rarely with a vertical ventral keel, constricted at their insertion upon the column, 1.5 mm. long. Ovaries 2 mm. long, glabrous; stigma-head cylindrical, shortly 2-fid. Follicles and seeds unknown.



*Sarcostemma Vaileae* is most closely related to *S. Gilliesii*. It may perhaps represent a race of that variable species which has become stabilized and no longer intergrades to an appreciable extent. Although the species are rather close morphologically, there is little difficulty in distinguishing them, for they differ not only in many vegetative characters but in several aspects of the flower as well. A general scarcity of pigmentation gives the stem, leaves, and flowers a characteristic pallid aspect. The column and anthers, on the other hand, are unusually dark, or even black, contrasting strongly with the white or yellow corona vesicles and corolla.

The collection, *Fiebrig 3084*, is the type of *Philibertia picta* Schltr. and is a form with dark flowers and light column. It is possibly a hybrid between *S. Vaileae* and *S. Gilliesii*, for the vegetative characters are those of the former species, but I prefer not to place the name in synonymy of either of these species at present. There are several collections, e. g. *Steinbach 8726*, which superficially match the type of *P. picta*, but which actually are easily referable to *S. solanoides* on the basis of the pubescence of the leaves, the character of the gynostegium, and the inflorescence.

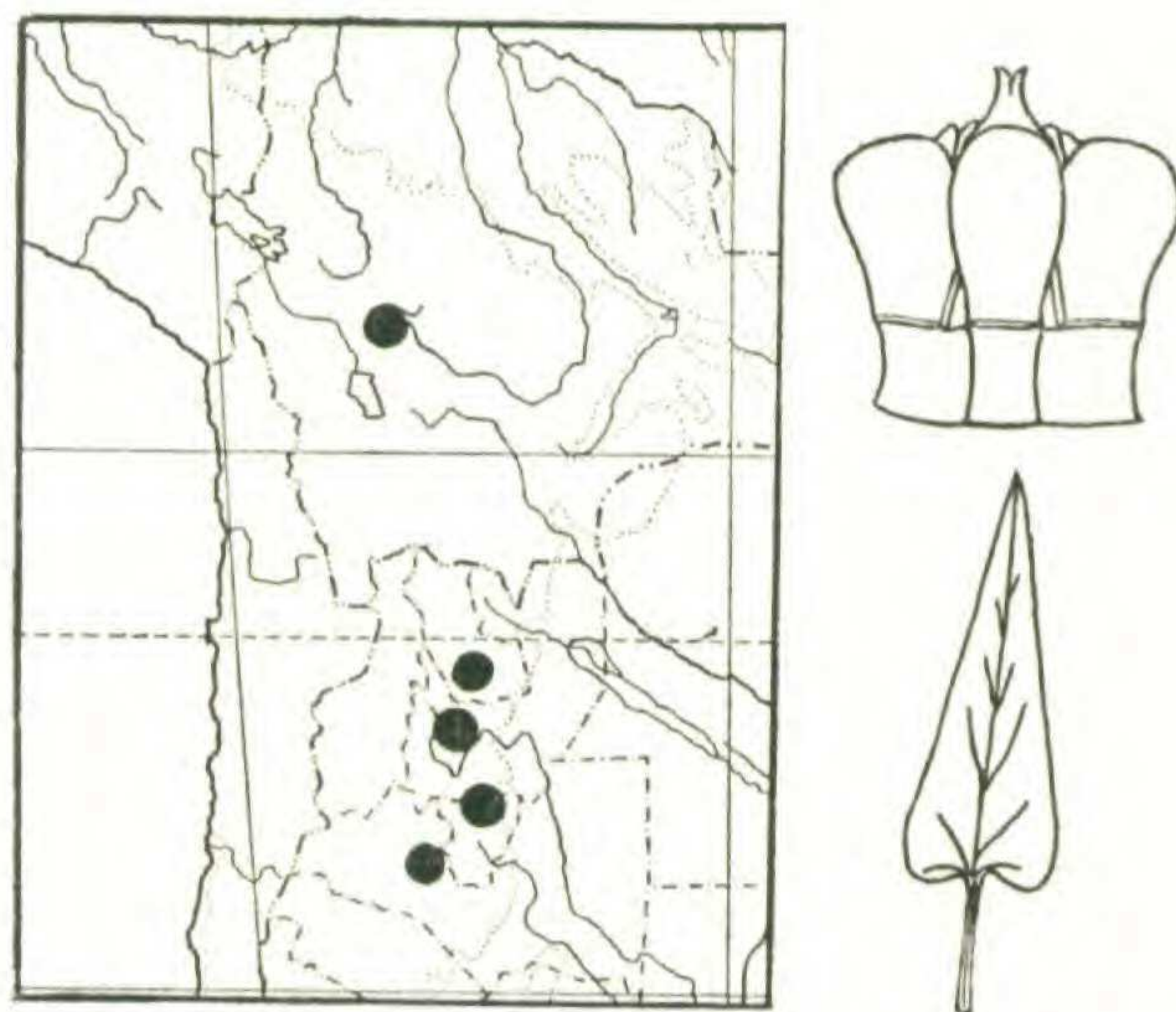


Fig. 20. Distribution, gynostegium, and leaf of *S. Vaileae*.

*Sarcostemma Vaileae* has been collected in Bolivia and northern Argentina in open woods at altitudes from 3500 feet to 6000 feet. Flowering specimens are dated December to March.

BOLIVIA. COCHABAMBA: Cochabamba, *Bang 985*, type of *Oxystelma Vaileae* Rusby.

ARGENTINA. CATAMARCA: Andalgalá, El Candado, *Jørgensen 1239*; Belén, Villavil, *Schreiter 10255*. JUJUY: Tumbaya, El Volcán, *Castillón 6473*. SALTA: Rosario de Lerma, Campo Quijano, *Venturi 8064*; Cerro San Bernardo, *West 6130*. TUCUMÁN: Trancas, San Pedro de Colalao, *Castillón 6781*.

18. *SARCOSTEMMA SOLANOIDES* (HBK.) Decne. in DC. Prodr. 8:541. 1844.

*Philibertia solanoides* HBK. Nov. Gen. et Sp. Pl. 3:196, t. 230. 1819. (T.: *Humboldt & Bonpland s. n. in Herb. Paris!*).

*Philibertia flava* Meyen, Reise 1:466. 1834, ex char.

*Pentagonium flavum* (Meyen) Schauer in Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1:364. 1843.



- Sarcostemma hastatum* Decne. loc. cit. 1844. (T.: *Dombey s. n. in Herb. Paris!*).  
*Sarcostemma marsupiflorum* Decne. loc. cit. 1844. (T.: *Cuming 983 in Herb. Kew!*).  
*Sarcostemma quadriflorum* Decne. loc. cit. 542. 1844. (T.: *Matthews 576 in Herb. Delessert!*).  
*Sarcostemma variifolium* Decne. loc. cit. 1844. (T.: *Dombey s. n. in Herb. Paris!*).  
*Oxystelma solanoides* (HBK.) K. Schum. in E. & P. Natur. Pflanzenfam. 4<sup>2</sup>:229. 1895.  
*Philibertia Weberbaueri* Schltr. in Engl. Bot. Jahrb. 37:607. 1906. (T.: *Weberbauer 2742 in Herb. Berol!*).  
*Philibertia quadriflora* (Decne.) Schltr. in Fedde's Repert. 13:282. 1915.  
*Philibertia variifolia* (Decne.) Schltr. loc. cit. 283. 1915.  
*Philibertia obtusiuscula* Malme, in Ark. Bot. 25A<sup>7</sup>:16, fig. 2. 1933. (T.: *Hicken 39 in Herb. Stockholm!*).  
*Philibertia obtusata* Malme, op. cit. 26A<sup>4</sup>:41. 1934, *sphalm.*

Stems twining or trailing, minutely puberulent; lateral branches many. Leaves ovate to deltoid-lanceolate, acute to acuminate, deeply cordate, the lobes diverging, 2.0–3.5 cm. long, 0.9–1.4 cm. wide, membranaceous to subcoriaceous, often somewhat undulate, scatteringly puberulent above, subtomentose beneath, with one or more glands on the midrib at the base; petiole 0.6–0.9 cm. long. Inflorescences umbelliform, 4- to 10-flowered; peduncle stout, slightly recurved at the apex, 3.5–7.5 cm. long, minutely puberulent; bracts linear, 0.1–0.2 cm. long; pedicels 0.9–1.3 cm. long, minutely puberulent. Calyx lobes narrowly lanceolate, 3–5 mm. long, scatteringly to densely puberulent without, glabrous within; squamellae absent, single, or paired. Corolla rotate-subcampanulate, greenish-yellow to cream with red or purple spots within, or uniformly greenish-yellow, the tube 5–6 mm. long, the lobes acute, 3–4 mm. long, puberulent without, glabrous within. Gynostegium 2–3 mm. high, vernicose, the column about 1 mm. long. Anthers 1.0–1.5 mm. long, the apical appendage deltoid, the pollinium-sacs compressed, obclavate, 0.5 mm. long, with sagittate corpusculum; ring of the corona short; vesicles of the corona truncate-oblongoid, with or without a small apiculation at the apex, 1.5 mm. long. Ovaries 2 mm. long, glabrous; stigma-head cylindrical, obscurely depressed or 2-lobed apically. Follicles ovoid, minutely puberulent, finely striate, 4.4 cm. long, 0.8 cm. thick; seeds unknown.

The umbelliform inflorescence and rotate-subcampanulate flowers at once distinguish this species from others of the subg. OXYSTELMA. Superficially, in fact, *S. solanoides* appears to pertain rather to the subg. CERAMANTHUS. This resemblance is most probably due to convergence, however, for not only the structure of the gynostegium, but also the detailed morphology of the inflorescences and vegetative organs relates it clearly to OXYSTELMA. The corona ring is very abbreviated and free from the corolla only at the outermost part, and the gynostegium is vernicose. The inflorescence, while umbelliform, is slightly recurved at the apex, a condition which does not obtain in subg. CERAMANTHUS.

*Sarcostemma solanoides* apparently is a trailing plant forming dense mats (but not rooting at the nodes), in dry, rocky, or gravelly soil or on talus slopes. In more favorable habitats it climbs into shrubs. It is reported that the herbage has an onion-like odor when crushed, presumably like that of *S. birtellum*. The species



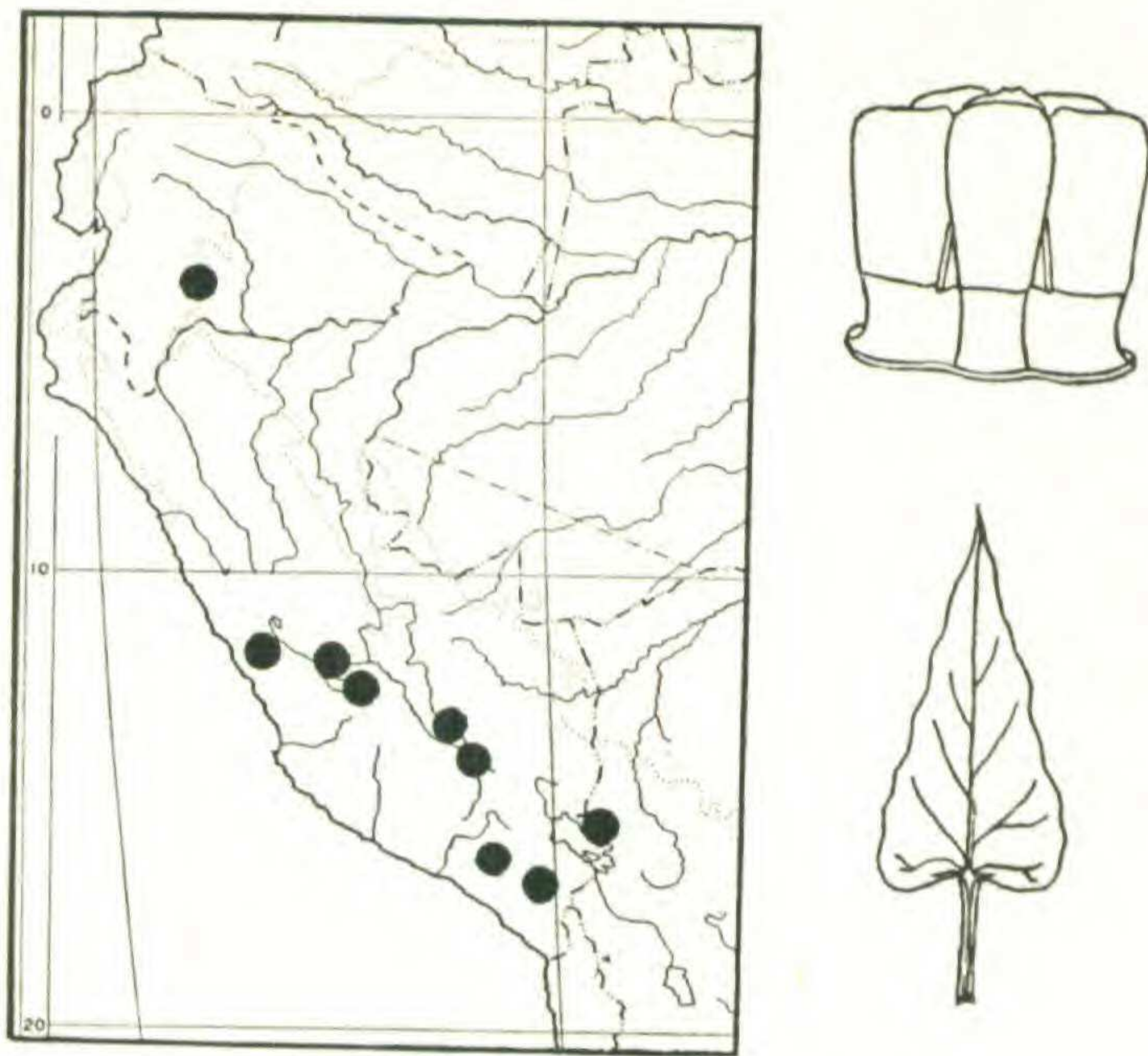


Fig. 21. Distribution, gynostegium, and leaf of *S. solanoides*.

ranges from southern Ecuador to northern Bolivia and has been collected in flower from February to April at altitudes from 6500 to 15000 feet.

ECUADOR. LOJA: between San Pedro & Chinchas, ca. 55 km. from Loja, *Espinosa* 1291; Hac. Huaico-Pamba, ca. 55 km. S Loja, *Espinosa* 2303.

PERU. AREQUIPA: Arequipa, *Pennell* 13195. CUZCO: Paruro, Huanquite, *Vargas* 2347; Cuzco, Callchaca, *Vargas* 5507; Canchis, slopes of Sicuani, *Vargas* 9829, *Stafford* 359; Sicuano, *Hicken* 39, type of *P. obtusiuscula* Malme. LIMA: Huarochiri, valley of Río Rimac, 81 km. E of Lima, *Goodspeed & Metcalf* 30229; Huarochiri Matucana, *Weberbauer* 5257, *Macbride* 2889, *Macbride & Featherstone* 208; Orroya near Lima, *Kalenborn* 30. HUANCAVELICA: Angaraes, 3 km. W of Huanta, *Stork & Horton* 10809; Tayacaja, Montaro Valley near La Mjorada, *Weberbauer* 7610; Tayacaja, Montaro Valley below Colabamba, *Weberbauer* 6453. LIMA: Río Blanco, *Macbride* 3042. MOQUEGUA: Carumas, *Weberbauer* 7298.

BOLIVIA. COCHABAMBA: Tal von Sacaba, *Steinbach* 8726. LA PAZ: near Sorata, *Mandon* 360.

19. *SARCOSTEMMA stipitatum* (Lillo) R. Holm, comb. nov.

*Philibertia stipitata* Lillo, in *Physis* 4:429. 1919. (T.: *Lillo* 2621 in *Herb. Lil'o!*).

Stems twining, glabrous or minutely pilosulose in lines decurrent from the petioles; lateral branches relatively few. Leaves lanceolate, acuminate, cordate, the lobes descending, 5.5–7.5 cm. long, 1.5–3.0 cm. wide, firmly membranaceous, undulate-crispate, essentially glabrous on both surfaces, the veins pilosulose, with one or more glands on the midrib at the base; petiole 1.0–2.5 cm. long. Inflorescences racemiform, 4- to 8-flowered; peduncle 3.0–5.8 cm. long, minutely appressed-pilosulose; bracts linear, 0.2–0.3 cm. long; pedicels 0.7–1.1 cm. long, minutely pilosulose. Calyx lobes narrowly lanceolate, 3.5 mm. long, appressed-pilosulose on both surfaces; squamellae few or absent, alternate. Corolla urceolate-campanulate, the tube 6 mm. long, the lobes bright brown, obtuse, 3 mm. long,



puberulent without, glabrous within. Gynostegium 3.5 mm. high, the column 1.5 mm. long. Anthers 1.5 mm. long, the apical appendage ovoid, slightly emarginate, the pollinium-sacs clavate-oblongoid, somewhat flattened, with a sterile hyaline region at the attachment of the translator arm, 0.75 mm. long, with narrowly ellipsoid corpusculum; ring of the corona nearly obsolete; vesicles of the corona oblate-spheroid, 1 mm. long. Ovaries 2 mm. long, glabrous, the styles well-marked; stigma-head cylindrical, obscurely depressed apically. Follicles and seeds unknown.

*Sarcostemma stipitatum* surely is the most distinctive species of the subg. OXYSTELMA, with its urceolate corolla, greatly reduced corona vesicles, and pollinia with a sterile, hyaline region, yet, surprisingly enough, it has never been referred to another genus. It is without obvious relationship to any other species to my knowledge. Rather sharply localized in northern Argentina, it grows at altitudes from 4500 to 5500 feet, and flowers from November to January.

ARGENTINA. SALTA: La Candelaria, Cuesta del Unquillo, *Schreiter* 9372. TUCUMÁN: Tafi, La Hoyada, *Venturi* 1536; Quebrada del Durasnillo, *Lillo* 2621, *Schreiter* 8703; Tafi, Cumbre del Siambón, *Venturi* 2821.

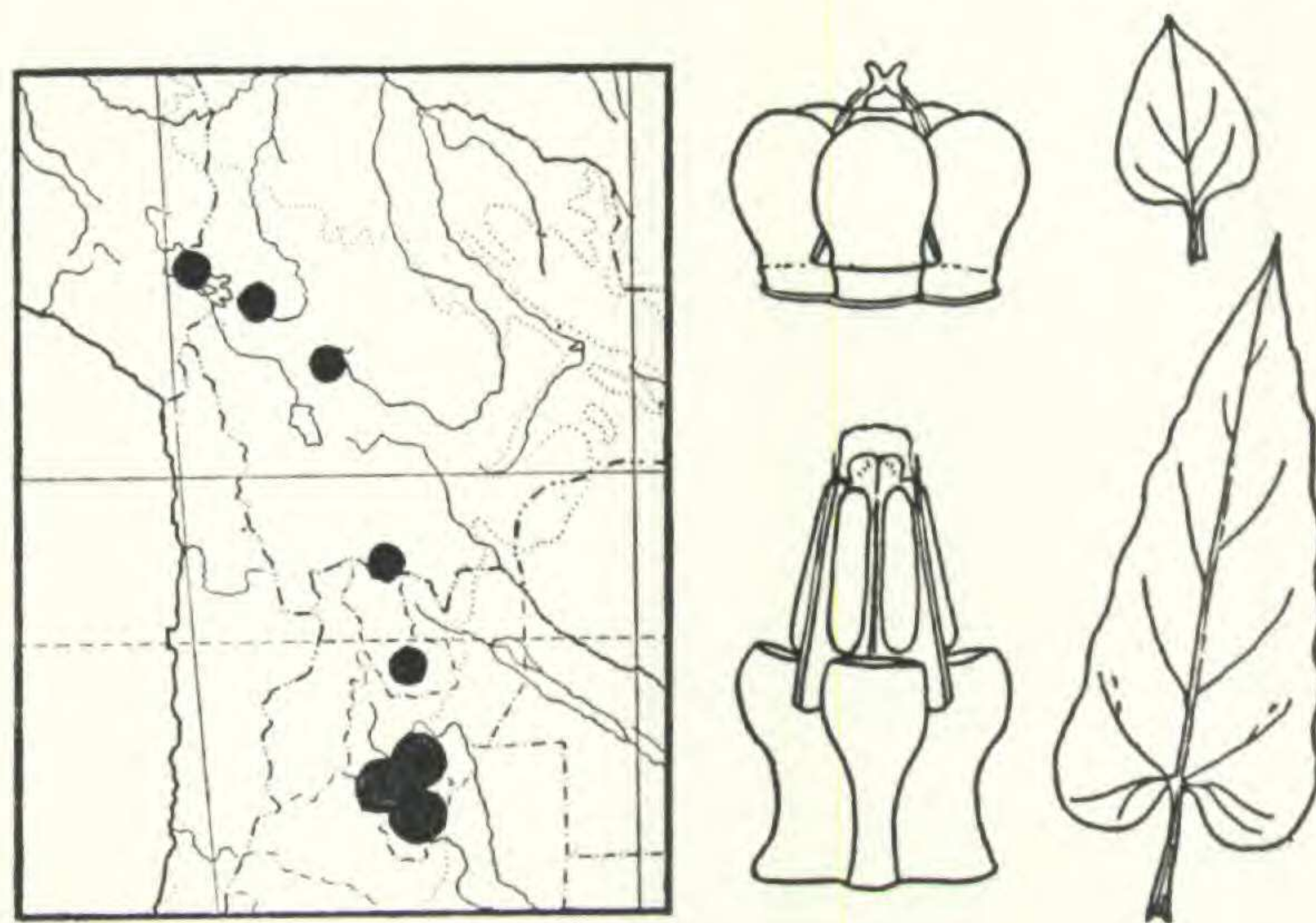


Fig. 22. Distribution of *S. stipitatum* (small dots), of *S. lysimachioides* (large dots). Gynostegium and leaf of *S. lysimachioides* (upper figures), of *S. stipitatum* (lower figures).

## 20. SARCOSTEMMA *lysimachioides* (Wedd.) R. Holm, comb. nov.

*Lugonia lysimachioides* Wedd. Chlor. And. 2:49, t. 54. 1857. (T.: *Weddell* 4136 in *Herb. Paris!*).

*Philibertia lysimachioides* (Wedd.) T. Meyer in Descole, Gen. et Sp. Pl. Arg. 2:177. 1944.

Stems prostrate, trailing from a short woody caudex, more or less articulate, minutely appressed-pilosulose; lateral branches many on the old stems. Leaves ovate, acute to obtuse, usually cordate, sometimes truncate or obtuse, 0.4–1.0 cm. long, 0.3–0.6 cm. wide, subcoriaceous, revolute, essentially glabrous on both sur-



faces, the midrib puberulous, usually without glands at the base (rarely a very few); petiole 0.2–0.4 cm. long. Inflorescences racemiform, 1- to 3-flowered; peduncle 0.4–0.7 cm. long, minutely pilosulose; bracts linear, 0.1–0.2 cm. long; pedicels 0.3–1.0 cm. long, appressed-pilosulose. Calyx lobes lanceolate to oblanceolate, 4 mm. long, puberulent without, glabrous within; squamellae alternate, 3–5, upon a thickened pad. Corolla campanulate, the tube 5.5 mm. long, the lobes deep orange to red, ovate, broadly obtuse, 5.5–6.0 mm. long, scatteringly puberulent without, glabrous within. Gynostegium 3 mm. high, the column 0.5 mm. long. Anthers 1.5 mm. long, the apical appendage deltoid, the pollinium-sacs clavate, 0.5 mm. long, with sagittate corpusculum; ring of the corona obsolete; vesicles of the corona ovoid, slightly constricted at their insertion upon the column, 1 mm. long. Ovaries 2 mm. long, glabrous, the styles well-marked; stigma-head conical, 2-apiculate, the apiculae flattened. Follicles fusiform, 1.9 cm. long, 0.3 cm. thick, minutely puberulent, finely striate; seeds unequally biconvex, 3 mm. long, 1.5 mm. wide, rugose on both surfaces, the margin entire; coma about 0.8 cm. long.

A plant of pronounced alpine modification, *S. lysimachioides* grows at heights of 9000 to 14000 feet in the Andes of Peru, Bolivia, and Argentina. It is a prostrate, perennial herb forming clumps among bunch grasses and shrubs. To precisely which species of *Sarcostemma* it is most closely related I am unable to determine. The corolla and gynostegium are reminiscent of *S. solanoides*, but the fact that the corolla is adnate to the column forms a clear distinction. This condition otherwise is found only in *S. andinum*, yet despite the fact that the latter and *S. lysimachioides* were included in the same segregate genus (*Lugonia*) in the past, I feel that they are only distantly related. *Sarcostemma lysimachioides* has been found in flower from November to February, and in fruit in April.

PERU. PUNO: Baja Isla del Lago Titicaca, *Mexia* 7789; Granja Salcedo, Cañon of Viscachani, *Mexia* 04261.

BOLIVIA. AYOPAYA: Weddell 4136, type of *L. lysimachioides* Wedd. CHUQUISACA: Tomina, Weddell s. n., 3885; Cinti, Weddell 3938. COCHABAMBA: Cochabamba, Weddell 4102; Ansaldo, Cárdenas 2292. LA PAZ: La Paz, Buchtien 67; Omasuyos, Mandon 359. TARIJA: about 45 km. NE of Villazón on Villa Montes, West 8234; Escayache bei Tarija, Fiebrig 3033.

ARGENTINA. JUJUY: Tumbaya, Mula Muerta, *Castillón* 6665.

#### Section 2. PENTACYPHUS (Schltr.) R. Holm, stat. nov.

*Pentacyphus* Schltr. in Engl. Bot. Jahrb. 37:605, fig. 3. 1906, as genus.

This section includes two species in which the corolla tube is adnate to the column and pubescent within, forming five hairy pouches alternating with the stamens. The column has deep grooves, and the large flowers have broadly obtuse corolla lobes.



## KEY TO THE SPECIES

- a. Leaves oblong-lanceolate, cordate; inflorescences racemiform, 2-flowered;  
corona segments undivided, depressed dorsally..... 21. *S. andinum*  
aa. Leaves obovate-elliptic, cuneate; inflorescences umbelliform, several-  
flowered; corona segments bipartite..... 22. *S. Lehmannii*

21. *SARCOSTEMMA andinum* (Ball) R. Holm, comb. nov.

*Lugonia andina* Ball, in Jour. Linn. Soc. Lond. 22:49. 1887. (T.: Ball s. n. in Herb. Kew!).

*Pentacyphus boliviensis* Schltr. in Engl. Bot. Jahrb. 37:605, fig. 3. 1906, ex char. (T.: Weberbauer 179 in Herb. Berol.).

Stems twining, glabrous or pilosulose in lines decurrent from the petioles; lateral branches many. Leaves oblong-lanceolate, acute to mucronate, cordate, the lobes descending, 1.5–5.0 cm. long, 0.6–2.4 cm. wide, membranaceous, glabrous above, the veins pilosulose, with one or more glands on the midrib at the base, appressed-pilosulose beneath; petiole 0.6–2.5 cm. long. Inflorescences racemiform, consisting of two 1-flowered cymules; peduncle 1–2 cm. long, minutely pilosulose; bracts linear, minute; pedicels 0.5–1.5 cm. long, minutely puberulent. Calyx lobes narrowly lanceolate, 8 mm. long, sparsely puberulent without, glabrous within, ciliolate; squamellae absent. Corolla campanulate, green to yellow, the lobes with a purple to dark red spot at the base, the tube 9.5 mm. long, glabrous without, pilosulose within, adnate to the column directly below the anthers forming five hairy pouches, each with a tuft of longer hairs borne upon a thickened pad at the base, the lobes broadly ovate, obtuse, 9 mm. long, glabrous on both surfaces. Gynostegium 7 mm. high, the column 4 mm. long, grooved between the stamens with the margins of the groove produced and arrect. Anthers 1.5 mm. long, the apical appendage oblong, mucronate, the pollinium-sacs oblongoid, somewhat flattened, 0.75 mm. long, with ellipsoid-sagittate corpusculum; ring of the corona obsolete; vesicles of the corona obovoid, depressed dorsally toward the apex, attenuate, 3 mm. long. Ovaries 4 mm. long, glabrous, the styles not well-marked; stigma-head 2-lobed. Follicles and seeds unknown.

*Sarcostemma andinum* has diverged markedly in a number of ways from the general OXYSTELMA type. The corolla is adnate to the column along five lines directly below the anthers; below the point of attachment the corolla tube is pilosulose within, so that five hairy pouches are formed. Exterior to these, the corolla is quite glabrous. The highly vernicose gynostegium is similarly extreme: as in several species of the subg. CERAMANTHUS, the column is grooved or invaginated directly below the anther wings, but in this case, the margins of the groove are produced at an angle of about 45° to the column. Continuous with the anther wings they, in effect, extend the latter the length of the column, down into the pouches, to the base of the corolla. Such modifications surely must adapt the flower very specifically to its insect pollinator.

These distinctive features of the plant, together with others of the inflorescence and pollinia, preclude relating *S. andinum* to any other species in the family except *S. Lehmannii*. The latter species is so distinct that it also has been considered, with



a certain justification, as a representative of a monotypic genus. I see no advantage in maintaining monotypic genera for such plants, however. To include them within another genus, separating them from the other species with appropriate subgeneric categories, at least indicates their affinities in a general way. Isolating them in a family with no adequate system of tribes conveys nothing as to their relationships, morphological or otherwise, and makes identification immeasurably more difficult.

*Sarcostemma andinum* is a widespreading vine, which grows in shady or open situations, climbing over shrubs and trees. It has been collected at altitudes from 5500 to 13000 feet; flowering specimens are dated from February to June.

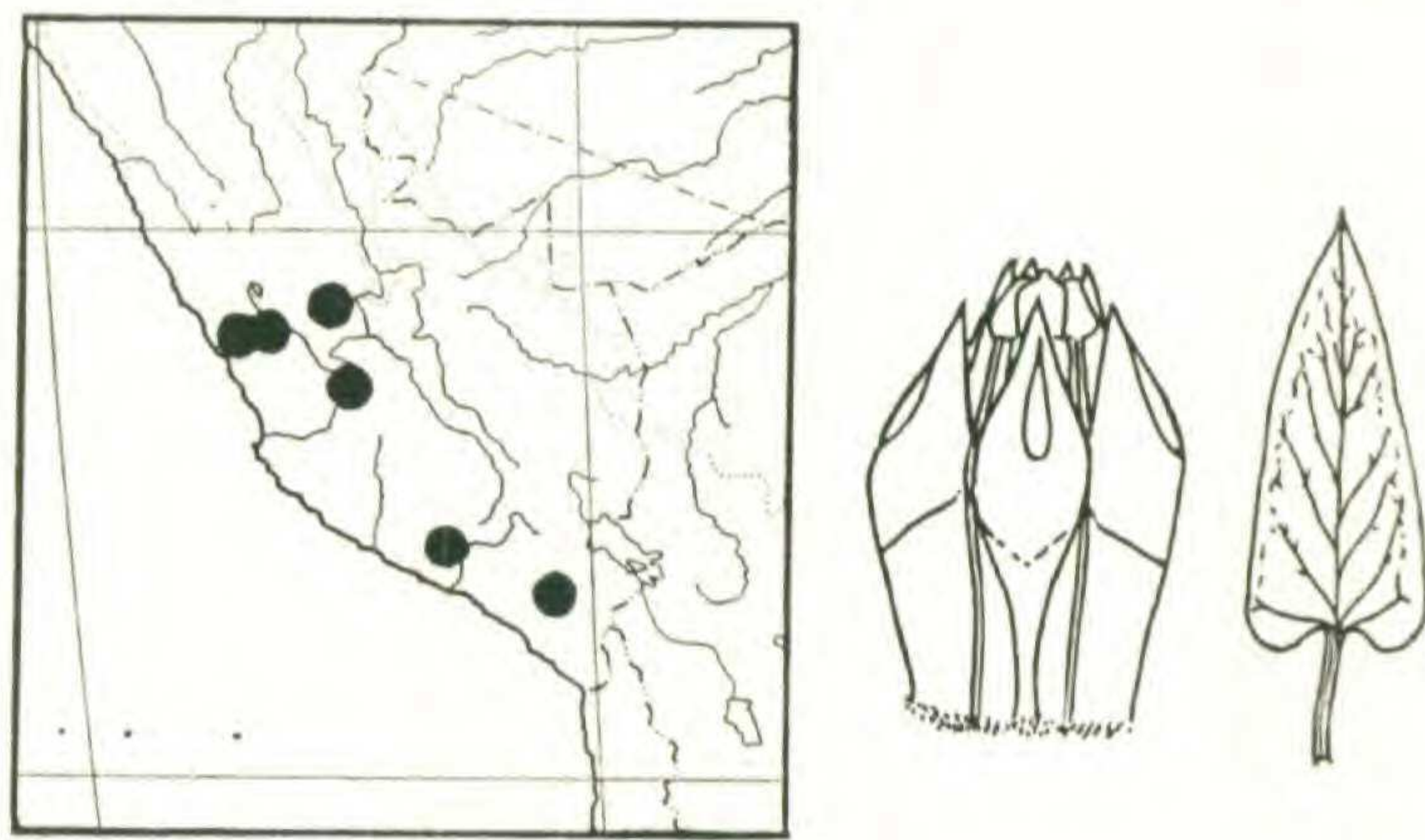


Fig. 23. Distribution, gynostegium, and leaf of *S. andinum*.

PERU. AREQUIPA: *Weberbauer* 6860. HUANCABELICA: *Castrovirreina*, near Córdoba, *Metcalf* 30274. LIMA: Huarochiri, valley of Río Rimac, 50 km. E of Lima, *Goodspeed* 33090; Huarochiri, Infiernillo, *Goodspeed, Stork & Horton* 11602; Huaros, *Pennell* 14722; Río Blanco, *Killip & Smith* 21701, *Macbride & Featherstone* 725; Matucana, *Macbride* 2951; near Lima, *Kalenborn* 30; Chicla, *J. Ball* s. n., type of *L. andina* Ball. MOQUEGUA: Carumas, *Weberbauer* 7258.

22. *SARCOSTEMMA Lehmannii* (Schltr.) R. Holm, comb. nov.

*Tetraphysa Lehmannii* Schltr. in Engl. Bot. Jahrb. 37:616. 1906, ex char. (T.: *Lehmann* 8516 in Herb. Berol.).

Stems twining, more or less articulate, glabrous; lateral branches few. Leaves obovate-elliptic, acute, cuneate, 9.5 cm. long, 4.0 cm. wide, coriaceous, glabrate, with several glands on the midrib at the base; petiole 1.5 cm. long. Inflorescences umbelliform, several-flowered; peduncle 2 cm. long, glabrous; bracts linear-lanceolate, 0.3–0.4 cm. long; pedicels 2.5 cm. long, glabrous. Calyx lobes obovate-elliptic, 7 mm. long, glabrous on both surfaces; squamellae alternate, solitary. Corolla campanulate, cream with reddish-purple spots within, the tube 7 mm. long, glabrous without, pilosulose within, adnate to the column directly below the anthers forming five hairy pouches, the lobes broadly ovate, obtuse, 15 mm. long, glabrous without, glabrous to minutely pilosulose within. Gynostegium 7 mm. high, the column 4 mm. long, grooved between the stamens (with the margins of



the groove slightly produced) and directly below the corona vesicles. Anthers 1.5 mm. long, the apical appendage oblong, the pollinium-sacs oblongoid, somewhat flattened, 0.5 mm. long, with ellipsoid corpusculum; ring of the corona obsolete; vesicles of the corona bipartite, consisting of two somewhat flattened, ovate, attenuate segments, joined toward the apex, exceeding the stigma-head in length. Ovaries 3 mm. long, glabrous, the styles not well-marked; stigma-head 2-lobed. Follicles and seeds unknown.

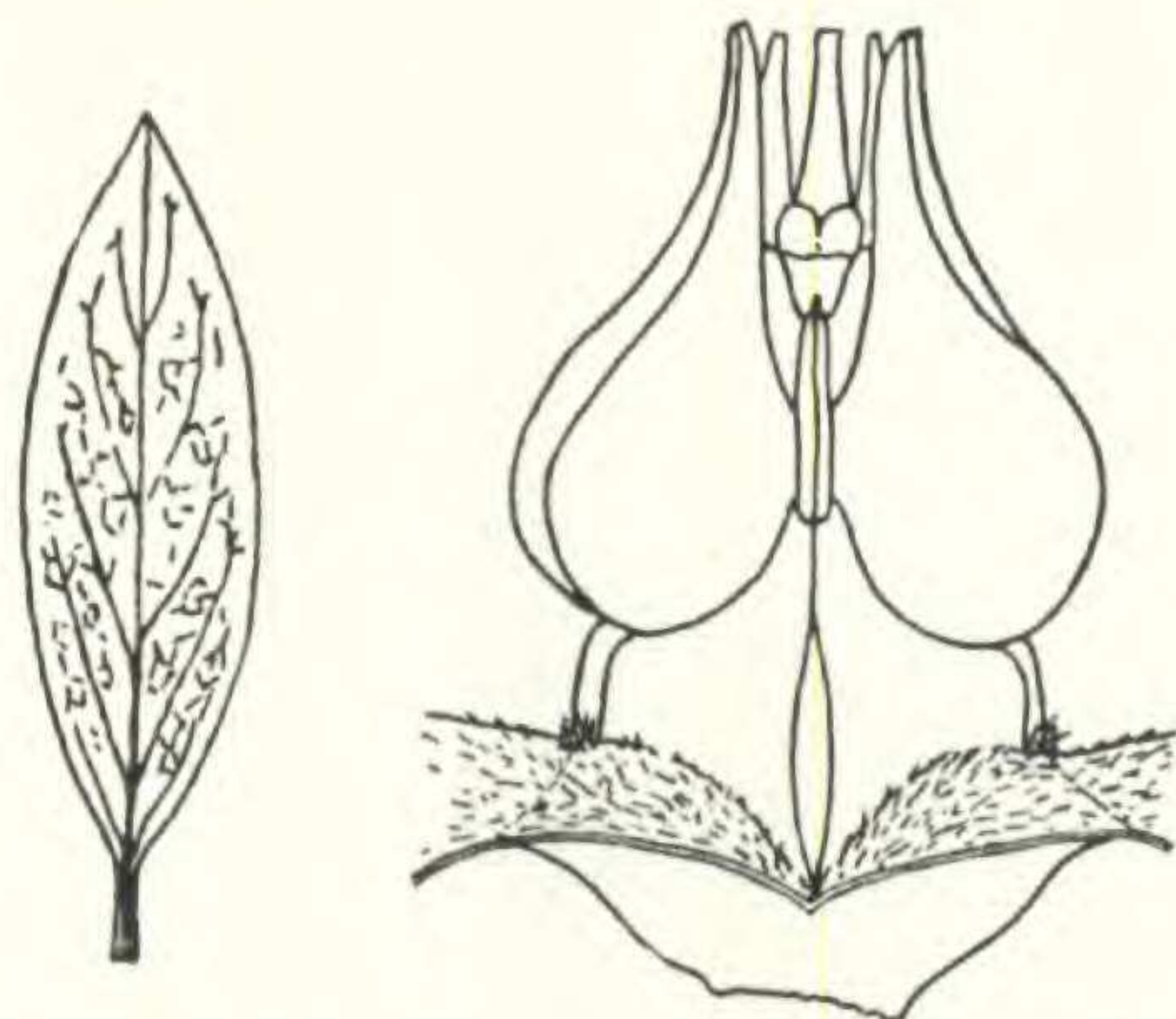


Fig. 24. Leaf and gynostegium of *S. Lehmannii*.

A most rare and distinctive species. I have not seen the type, but the description and figures of Schlechter leave no doubt as to its identity with the single subsequent collection available to me. The gynostegium is highly vernicose and superficially similar to that of *Sarcostemma andinum*. In addition to the five grooves in the column which lead into the pouches of the corolla tube, there are five longitudinal clefts which divide the corona vesicles, and the column directly below them, to the corolla. As I have indicated in the discussion of the preceding species, *S. Lehmannii* is probably most closely related to *S. andinum*. The evolution of the gynostegium may be pictured as involving an extension of the dorsal depression of the corona vesicles of the latter species, until it extends to the corolla. The advantages of such an arrangement to the plant are not in the least apparent, however. If these forms are to be related to any group in the Asclepiadaceae, it must surely be to *Sarcostemma*. I have merged them with that genus, indicating their divergence by sectional segregation, rather than let them drift among the many other monotypic genera without obvious mooring.

*Sarcostemma Lehmannii* has been collected in dense woods at altitudes of about 8000 feet, and was in flower in May and October.

COLOMBIA. CAUCA: vicinity of Popayan, *Lehmann 8516*, type of *T. Lehmannii* Schltr., not seen.

ECUADOR. LOJA: between Tambo Cachiya, La Entrada, and Nudo de Sabanillas, *Steyermark 54471*.

#### IMPERFECTLY KNOWN SPECIES

*Sarcostemma Jacquini* Decne. in DC. Prodr. 8:542. 1844. Description inadequate, no type cited.

*Sarcostemma trichopetalum* Alv. Silv., Fl. Serr. Mineir. 18. 1908. Publication unavailable to me.



## EXCLUDED SPECIES

- Philibertia anomala* T. S. Brandeg. in Univ. Calif. Publ. Bot. 4:277. 1912.  
 = BLEPHARODON MUCRONATUM (Schlecht.) Decne.  
*Lugonia micrantha* Malme, in Nova Acta Acad. Soc. Upsal. IV, 1<sup>1</sup>:115. 1905.  
 = APHANOSTELMA MICRANTHUM (Malme) T. Meyer.  
*Philibertia* ? *scandens* Gomez, in Anal. Hist. Nat. Madrid 23:276. 1894.  
 = FISCHERIA SCANDENS DC.  
*Philibertia viridiflora* (Torr.) Britt. & Rusby, in Trans. N. Y. Acad. Sci. 7:11. 1887, sphalm.

## INDEX TO EXSICCATAE

*Italicized* numbers refer to the collectors' numbers, *s. n.* (*sine numero*) to unnumbered collections; parenthetical numerals indicate the numbers of the taxonomic entities recognized in this monograph. Only specimens from the Western Hemisphere are included.

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